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THE EFFECTS OF CLIMATE CHANGE AND NITROGEN DEPOSITION ON THE LIMNOLOGY OF ALPINE PONDS

by

Natalie Lynn McMaster

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
Masters of Science

in

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Faculty of Graduate Studies and Research

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ABSTRACT

Alpine ponds may be particularly sensitive to environmental change yet their limnology is poorly described. I described the limnology and determined how climate change and nitrogen deposition may affect the physical and chemical features and algal communities in alpine ponds. By studying the physical and chemical limnology in five alpine ponds through a warm-dry and a cold-wet ice-free season I determined that they are physically demanding aquatic ecosystems which may become even more extreme with climate warming as water temperatures, extreme temperature events, ice-free periods, drying rates, base cations, alkalinity, pH and conductivity increase. I surveyed the physical and chemical features, and planktonic and epipelic algal communities in 28 alpine ponds and found that TP, NO_2-N+NO_3–N, pH, conductivity, and DOC were important predictors of algal communities but that predictors vary annually. Epilithic algal growth on nutrient diffusing substrata was primarily N-limited suggesting that alpine ponds may be vulnerable to increased anthropogenic N deposition.

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CHAPTER 1: GENERAL INTRODUCTION

Climate change and nitrogen deposition affect the physical, chemical and biological features of aquatic systems. Alpine sites experience enhanced climate warming and alpine ecosystems are particularly sensitive to nitrogen deposition. However, little is known about alpine limnology, especially alpine pond limnology. The objective of this study was to describe the limnology of alpine ponds and determine how changing global stressors, in particular climate change and nitrogen deposition may affect physical and chemical features and algal communities of alpine ponds.

Climate change and its effects on aquatic ecosystems

In the last century, the global climate has warmed significantly, at a faster rate than any other century in the last 1000 years (Mann et al. 1999). Southern Canada's climate has warmed by an average of 0.8 °C in the 20th century (Zhang *et al.* 2000) and Banff town site's climate has warmed by 1.4 °C in the 20th century (Luckman 1998). This warming trend is predicted to continue in the future (Intergovernmental Panel on Climate Change 2001) and high elevation sites are predicted to warm even faster than low elevation sites because they are in more direct contact with the free troposphere and are therefore less affected by the cooling effects of local pollution (Giorgi et al. 1997; Fyfe and Flato 1999). In addition, warmer temperatures reduce permanent snowpack at high elevation sites and therefore reduce surface albedo, which results in even warmer temperatures (Giorgi et al. 1997). Enhanced warming at high elevation sites has been documented in the European Alps (Beniston et al. 1994) and is of particular concern since high elevation ecology, in particular alpine limnology, is largely unstudied.

Despite the enhanced warming in high elevation sites, many of the predicted effects of climate warming on alpine aquatic ecosystems remain speculative and are based on trends found in low elevation regions (Hauer et al. 1997; Schindler 1997; Skjelkvale and Wright 1998). However, during a decade of climate warming, European alpine lakes became warmer and had more sulfate, base cations and silica and less inorganic nitrogen (Sommaruga-Wögrath et al. 1997). Diatom assemblages were also altered (Sommaruga-

Wögrath et al. 1997). In other alpine lakes in the Alps, pH increased with temperature (Psenner and Schmidt 1992; Koinig et al. 1998). Many of these changes were similar to those found in low elevation sites (Schindler et al. 1996) but climate warming may have greater physical, chemical and biological effects in alpine ecosystems because snow and ice cover, which are extremely sensitive to changes in climate, play a predominant role in the hydrology and biogeochemistry in alpine ecosystems (Koinig et al. 1998; Bowman 2000).

Of the aquatic ecosystems, ponds are expected to be particularly sensitive to climate change due to their dynamic water budgets and small surface areas and depths. Water budgets of most ponds depend on snow melt and atmospheric processes such as precipitation and evapotranspiration (Hartland-Rowe 1972). Therefore their water levels and subsequently their physical, chemical and biological features are very responsive to any change in climate (Girdner and Larson 1995; Lahr 1997). Furthermore, because ponds are small and shallow they have limited capacity for heat storage and consequently their water temperatures mimic air temperatures (Daborn 1976). This sensitivity of ponds to climate has resulted in an abundance of research on arctic ponds and climate change (Douglas et al. 1994; Douglas and Smol 1999; Lim et al. 2001; Michelutti et al. 2002). However, it is still unknown how alpine ponds will respond to climate change.

Nitrogen deposition and its effects on aquatic ecosystems

Atmospheric nitrogen (N) has increased regionally as a result of human activities such as fossil fuel combustion and fertilizer application (Vitousek et al. 1997). In the case of the Canadian Rocky Mountains, annual wet nitrate deposition has increased from under 1.7 to over 2.4 kg ha^{-1} yr^{-1} over the last 15 years in the south-eastern front ranges (Kananaskis Country, 1403 meters above sea level; Alberta Environment 2003). This excess N can lead to terrestrial N-saturation and consequently increased N loading to aquatic ecosystems (Bowman and Steltzer 1998). High elevation watersheds are particularly responsive to terrestrial N-saturation and increased atmospheric N deposition because their steep, sparsely vegetated watersheds readily transport N (Williams et al. 1996; Baron et al. 2000; Campbell et al. 2000; Sickman 2001).

Mountain lakes in the western United States are predominantly N-limited (Morris and Lewis 1988; Goldman et al. 1993; Axler and Reuter 1996; Interlandi et al. 1999; Sickman 2001; Lafrançois 2002). Increased N loading to these N-limited lakes has increased algal productivity and biomass and altered species composition (Goldman et al. 1993; Wolfe et al. 2001; Lafrançois 2002) and thus affected the entire food web. The extent of N-limitation and therefore the effects of increased N loading may be significant for alpine ponds in the Canadian Rocky Mountains.

Alpine pond limnology

Alpine ponds are numerous in the Canadian Rocky Mountains, with over 3000 located in Banff National Park (6,641 km^2). Despite their abundance, only five studies have been published since North American alpine ponds were classified and described by Ives in 1941. In the Colorado Rocky Mountains, very basic seasonal limnological changes were described in one large alpine (Neldner and Pennak 1955) and two small alpine ponds (Schmitz 1959). Based on these studies alpine ponds were similar to ponds at lower elevations in that they have dynamic water budgets, limited thermal stratification and seasonally variable chemical characteristics (Neldner and Pennak 1955; Schmitz 1959). Phytoplankton and zooplankton species richness were low and species of Anostraca, Trichoptera, Coleoptera and Hemiptera were abundant compared to surrounding lakes (Neldner and Pennak 1955; Schmitz 1959). Alpine ponds differed from low elevation ponds in that they had short growing seasons (<100 days) and lacked macrophytes (Neldner and Pennak 1955; Schmitz 1959). Although not observed, alpine ponds were assumed to freeze to the bottom in the winter.

In the Canadian Rocky Mountains, planktonic crustaceans were surveyed in 14 alpine ponds (Anderson 1971; 1974) and planktonic and benthic algal communities were surveyed in two alpine ponds (Vinebrooke and Leavitt 1999). Crustacean species richness was similar in alpine ponds and lakes but anostracans and five large crustaceans were endemic to ponds (Anderson 1971; 1974). Based on two alpine ponds, algal biomass was less but communities were similar to alpine lakes (Vinebrooke and Leavitt 1999). The

lack of research on alpine ponds is due to both the logistical challenges of working in the alpine and the tendency for limnologists to study larger systems. However as anthropogenic influences such as climate change and nitrogen deposition intensify in high elevation regions (Baron et al. 2000; Luckman and Kavanagh 2000) understanding the limnology of alpine aquatic systems has become a priority (Schindler 2000).

Objectives and methods

My main objectives are to:

1. Describe the physical and chemical features of alpine ponds and predict how these features may respond to climate change (Chapter 2).
2. Describe the basic limnology across 28 alpine ponds and predict how the algal communities may respond to nutrient deposition and climate change (Chapter 3).
3. Describe the epilithic algal community and determine how nitrogen deposition may affect alpine pond communities (Chapter 4).

To achieve the first objective, I recorded 21 physical and chemical variables in five ponds through a warm-dry (1998) and a cold-wet (1999) ice-free season. The more specific objectives for this chapter included:

A) Describe the seasonal physical and chemical limnology of alpine ponds.

B) Compare the physical and chemical limnology of alpine ponds to arctic ponds in Alaska, United States (Hobbie 1980) and Nunavut, Canada (Douglas and Smol 1994).

C) Determine how climate change may affect the physical and chemical limnology of alpine ponds. Therefore I determined: 1) how important were air temperature and precipitation in controlling the freeze-thaw cycle, water budget, water temperature and water chemistry of alpine ponds; and 2) if the physical and chemical features of alpine ponds differ between a warm-dry year (1998) and a cold-wet year (1999).

To achieve the second objective, I surveyed 14 ponds in 1999 and 28 ponds in 2000 and recorded 15 physical and chemical variables and sampled planktonic and epipelic (sediment-living) algal community pigments using high performance liquid

chromatography (HPLC) in each pond. The more specific objectives for this chapter included:

A) Describe the physical and chemical limnology across 28 alpine ponds; assess nutrient limitation with nitrogen to phosphorus ratios; and describe the phytoplankton and epipelon communities across 28 alpine ponds in Banff National Park.

B) Identify the physical and chemical variables that best explain phytoplankton and epipelon abundance and community composition in alpine ponds.

C) Determine if the physical and chemical variables that best explain these patterns differ between two summers.

To achieve the third objective, I used nutrient diffusing substrata (NDS) to control nutrient supply and invertebrate colonization in early and mid-summer in three alpine ponds. After five weeks, epilithon (sediment-dwelling) abundance and community structure were assessed using pigments analyzed by HPLC. The more specific objectives for this chapter included:

A) Determine if epilithon abundance and community composition in pristine alpine ponds respond to nitrogen inputs (i.e., N-limitation).

B) Determine if the nutrient effects depend on grazing pressure (i.e., nutrient-grazer interaction).

C) Determine if the individual and interactive nutrient and grazer effects are time-dependent over the ice-free season.

REFERENCES

Alberta Environment. 2003. Unpublished database. Evaluation and Reporting Section. Environmental Monitoring and Evaluation Branch. 9820 - 106 Street, Edmonton, Alberta, Canada.

Anderson, R.S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in Western Canada. Journal of Fisheries Research Board of Canada **28**: 311-321.

Anderson, R.S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. Journal of the Fisheries Research Board of Canada **31**: 855-869.

Axler, R.P. and Reuter, J.E. 1996. Nitrate uptake by phytoplankton and periphyton: Whole lake enrichment and mesocosm ^{15}N experiment in an oligotrophic lake. Limnology and Oceanography **41**: 659-671.

Baron, J.A., Rueth, H.M., Wolfe, A.M., Nydick, K.R., Allstott, E.J., Minear, J.T. and Moraska, B. 2000. Ecosystem response to nitrogen deposition in the Colorado Front Range. Ecosystems **3**: 352-368.

Beniston, M., Rebetez, M., Giorgi, F. and Marinucci, M.R. 1994. An analysis of regional climate change in Switzerland. Theoretical and Applied Climatology **49**: 135-159.

Bowman, W.D. 2000. Biotic controls over ecosystem response to environmental change in alpine tundra of the Rocky Mountains. Ambio **29**: 396-400.

Bowman, W.D. and Steltzer, H. 1998. Positive feedback to anthropogenic nitrogen deposition in Rocky Mountain Alpine Tundra. Ambio **27**: 514-517.

Campbell, D.H., Baron, J.A., Tonnessen, K.A., Brooks, P.S. and Schuster, P.F. 2000. Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resources Research **36**: 37-47.

Daborn, G.R. 1976. Physical and chemical features of a vernal temporary pond in Western Canada. Hydrobiologia **51**: 33-38.

Douglas, M.S.V. and Smol, J.P. 1994. Limnology of high arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.). Archiv für Hydrobiologie **131**: 401-434.

Douglas, M.S.V. and Smol, J.P. 1999. Freshwater diatoms as indicators of environmental changes in the high Arctic. *In* The Diatoms: Applications for the Environmental and Earth Sciences. *Edited by* E.F. Stoermer and J.P. Smol. Cambridge University Press, Cambridge. pp. 227-44.

Douglas, M.S.V., Smol, J.P. and Weston Blake, J.R. 1994. Marked post-18th century environmental change in high-Arctic ecosystems. Science **266**: 416-419.

Elser, J.J., Marzolf, E.R. and Goldman, C.R. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Canadian Journal of Fisheries and Aquatic Sciences **47**: 1468-1477.

Francoeur, S.N. 2001. Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. Journal of North American Benthological Society **20**: 358-368.

Fyfe, J.C. and Flato, G.M. 1999. Enhanced climate change and its detection over the Rocky Mountains. Journal of Climate **12:** 230-243.

Girdner, S.F. and Larson, G.L. 1995. Effects of hydrology on zooplankton communities in high-mountain ponds, Mount Rainer National Park, USA. Freshwater Biology **35**: 1731-1755.

Giorgi, F., Hurrell, J.W. and Marinucci, M.R. 1997. Elevation dependency of the surface climate change signal: A model study. Journal of Climate **10**: 288-296.

Goldman, C.R., Jassby, A.D. and Hackley, S.H. 1993. Decadal, interannual and seasonal variability in enrichment bioassays at Lake Tahoe, California-Nevada, USA. Canadian Journal of Fisheries and Aquatic Sciences **50:** 1489-1496.

Hartland-Rowe, R. 1972. The limnology of temporary waters and the ecology of Euphyllopoda. *In* Essay in Hydrobiology. *Edited by* P.B. Clarke and R. Wootton. University of Exeter, Devon, England. pp. 15-31.

Hauer, F.R., Baron, J.S., Campbell, D.H., Fausch, K.D., Hostetler, S.W., Leavesley, S.W., Leavitt, P.R., McKnight, D.M. and Stanford, J.A. 1997. Assessment of climate

change and freshwater ecosystems of the Rocky Mountains, US and Canada. Hydrological Processes **11**: 903-924.

Hobbie, J.E. 1980. Limnology of Tundra Ponds: Barrow Alaska. Dowden, Hutchinson and Ross, Inc., Pennsylvania, United States.

Intergovernmental Panel of Climate Change. 2001. Climate Change 2001: The Scientific Basis. http://www.grida.no/climate/ipcc_tar/wg1/index.htm

Interlandi, S.J., Kilham, S.S. and Theriot, E.C. 1999. Response of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. Limnology and Oceanography **44:** 668-682.

Koinig, K.A., Schmidt, R., Sommaruga-Wögraph, S., Tessadri, R. and Psenner, R. 1998. Climate change as the primary cause for pH shifts in a high alpine lake. Water, Air and Soil Pollution **104**: 167-180.

Lafrançois, B.M. 2002. Algal and invertebrate response to atmospheric nitrogen deposition in Rocky Mountain lakes. Ph.D. thesis, Colorado State University, Fort Collins, Colorado, United States.

Lahr, J. 1997. Ecotoxicology of organisms adapted to life in temporary freshwater ponds in arid and semi-arid regions. Archive of Environmental Contamination and Toxicology **32**: 50-57.

Lim, D.S.S., Douglas, M.S.V. and Smol, J.P. 2001. Diatoms and their relationships to environmental variable from lakes and ponds on Bathurst Island, Nunavut, Canadian High Arctic. Hydrobiologia **450**: 215-230.

Luckman, B.H. 1998. Landscape and climate change in the central Canadian Rockies during the 20th century. Canadian Geographer **42**: 319-336.

Luckman, B.H. and Kavanagh, T. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. Ambio **29**: 371-380.

Mann, M.E., Bradley, R.S. and Hughes, M.K. 1999. Northern Hemisphere temperatures during the past millennium: Inferences, uncertainties and limitations. Geophysical Research Letters **26**: 759-762.

Michelutti, N., Douglas, M.S.V., Muir, D.C.G., Wang, X. and Smol, J.P. 2002. Limnological characteristics of 38 lakes and ponds on Axel Heiberg Island, high arctic Canada. International Review of Hydrobiology **87**: 383-399.

Morris, D.P. and Lewis, W.M. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biology **20**: 315-327.

Neldner, K.N. and Pennak, R.W. 1955. Seasonal faunal variations in a Colorado alpine pond. American Midland Naturalist **53**: 419-430.

Psenner, R. and Schmidt, R. 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. Nature **356**: 781-783.

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. Hydrological Processes **11**: 1043-1067.

Schindler, D.W. 2000. Aquatic problems caused by human activities in Banff National Park, Alberta, Canada. Ambio **29**: 401-407.

Schindler, D.W., Bayley, S.E. and Parker, B.R. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, Northwestern Ontario. Limnology and Oceanography **41**: 1004-1017.

Schmitz, E.H. 1959. Seasonal biotic events in two Colorado alpine tundra ponds. The American Midland Naturalist **61**: 424-445.

Sickman, J.O. 2001. Comparative analysis of nitrogen biogeochemistry in high elevation ecosystems. Ph.D. thesis, University of California, Santa Barbara, California, United States.

Skjelkvale, B.L. and Wright, R.F. 1998. Mountain lakes: Sensitivity to acid deposition and global climate change. Ambio **27**: 280-286.

Sommaruga-Wögraph, S., Koinig, K.A., Schmidt, R., Sommaruga, R., Tessadri, R. and Psenner, R. 1997. Temperature effects on the acidity of remote alpine lakes. Nature **387**: 64-67.

Vinebrooke, R.D. and Leavitt, P.R. 1999. Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. Journal of North American Benthological Society **18**: 14-32.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. and Tilman, D.G. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications **7**: 737-750.

Williams, M.W., Baron, J.S., Caine, N., Sommerfeld, R. and Sanford, R. 1996. Nitrogen saturation in the Rocky Mountains. Environmental Science and Technology **30**: 640-646.

Wolfe, A.P., Baron, J.S. and Cornett, R.J. 2001. Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). Journal of Paleolimnology **25:** 1-7.

Zhang, X., Vincent, L.A., Hogg, W.D. and Niitsoo, A. 2000. Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38: 395-429.

CHAPTER 2: PHYSICAL AND CHEMICAL LIMNOLOGY OF ALPINE PONDS IN BANFF NATIONAL PARK, CANADA: POTENTIAL IMPACT OF CLIMATE CHANGE

INTRODUCTION

In the last century, global climate has warmed significantly and at a faster rate than any other century in the last 1000 years (Mann et al. 1999). Southern Canada's climate has warmed by an average of 0.8 °C in the 20th century (Zhang *et al.* 2000) and the warming trend is predicted to continue in the future (Intergovernmental Panel on Climate Change 2001). High elevation sites are predicted to warm even faster than low elevation sites (Giorgi et al. 1997; Fyfe and Flato 1999). Enhanced warming at high elevation sites has been documented in the European Alps (Beniston et al. 1994) and is of particular concern since high elevation ecology, in particular alpine limnology, is largely unstudied.

Climate affects both the physical (e.g., water budget, length of the ice-free season and temperature) and chemical (e.g., major ion and nutrient concentrations) features of lakes. Drastic changes in limnological features are predicted in response to climate change (Limnology and Oceanography 41 (5), 1996; Hydrological Processes 11 (8), 1997). For instance, during a prolonged warm-dry period in northwestern Ontario, boreal lakes not only had longer ice-free seasons and water renewal times but they also became warmer, clearer and contained less dissolved organic carbon, phosphorus and silica and more strong acid anions and base cations (Schindler et al. 1990; 1996).

Ponds may be particularly responsive to climate change due to their small surface area and shallow depth. In low elevation ponds, air temperature and precipitation affect water temperature and the rate and degree of drying which subsequently affect physical and chemical variables (e.g. depth, surface area, volume, light, dissolved oxygen, dissolved salts, pH) (Williams 1996; Lahr 1997). Furthermore, shallow arctic ponds are extremely sensitive to changes in air temperature and precipitation (Douglas and Smol 1999). Alpine ponds seemed likely to be similarly sensitive to climate change and located in a region predicted to have enhanced climate warming, causing us to undertake this study.

Alpine ponds are numerous in the Canadian Rocky Mountains. Over 3000 are located in Banff National Park (6,641 km^2). Despite their abundance, only three biological surveys have been conducted on Canadian Rocky Mountains alpine ponds (Anderson 1971; Anderson 1974; Vinebrooke and Leavitt 1999). Furthermore, the physical and chemical limnology of North American alpine ponds is known for only three Colorado Rocky Mountain ponds (Neldner and Pennak 1955; Schmitz 1959). However as anthropogenic influences, such as climate change, intensify in high elevation regions (Luckman and Kavanagh 2000), understanding the limnology of alpine aquatic systems has become a priority (Schindler 2000). It has been suggested that alpine ponds should be physically similar to arctic ponds because they share a similar physically harsh environment (Hobbie 1973; Hebert and Hann 1989) but a thorough comparison has not been completed.

The first objective was to describe the physical and chemical limnology of alpine ponds. I recorded 21 physical and chemical variables in five ponds through the 1998 and 1999 ice-free seasons. The second objective was to compare the physical and chemical limnology of alpine and arctic ponds. Therefore I compared my results to those from arctic ponds in Alaska, United States (Hobbie 1980) and Nunavut, Canada (Douglas and Smol 1994). The third objective was to determine how climate change may affect the physical and chemical limnology of alpine ponds. Therefore I determined: 1) how important were air temperature and precipitation in controlling the freeze-thaw cycle, water budget, water temperature and water chemistry of alpine ponds; and 2) if the physical and chemical features of alpine ponds differ between a warm-dry year (1998) and a cold-wet year (1999). This research will add to our existing knowledge of alpine ponds, provide baseline data to which future change can be compared and allow us to predict how the physical and chemical limnology of alpine ponds will respond to climate change.

METHODS

Study site

The study ponds are located on Snow Creek Summit (2300 m above sea level; 51°36'N, 115° 51'W) in the eastern front ranges of the Rocky Mountains in Banff National Park, Alberta, Canada (Figure 2.1). Pond catchments consist of a mosaic of small patches of

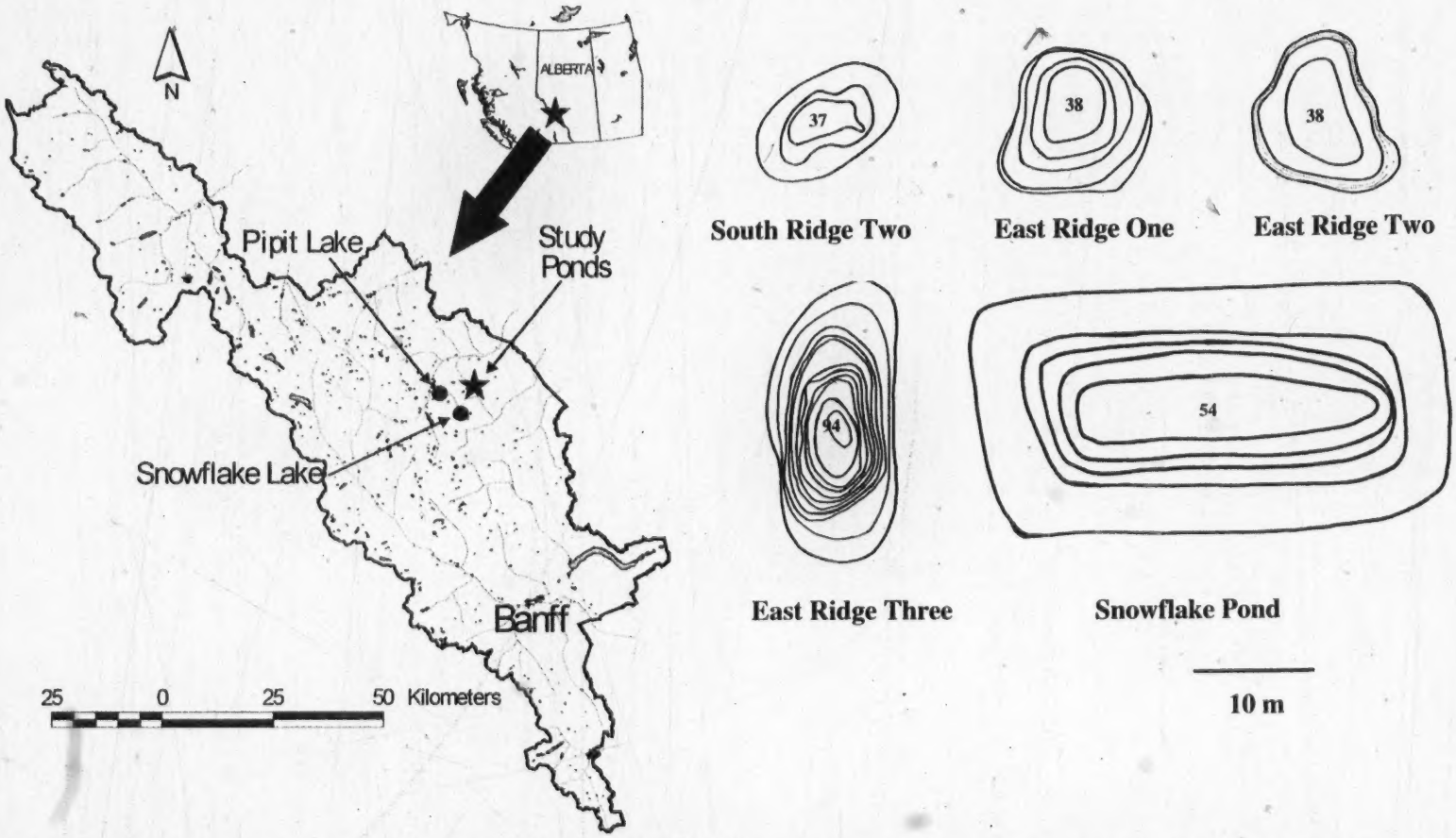


Figure 2.1: Study ponds are located on Snow Creek Summit (51°36'N, 115° 51'W) in Banff National Park, Alberta, Canada. Bathymetric maps of all study ponds are given with maximum depths and 5 cm contours. However, because the ponds had U-shaped basins I could not show all the contours and therefore the outside line represents a cluster of contours.

exposed sedimentary rock, including limestone, shale and sandstone, and sparsely vegetated pockets of orthic eutric brunisol soils (Holland and Coen 1982). Soils ranged from moderately acidic to mildly alkaline (pH > 5.5; Holland and Coen 1982). Vegetation on sites with soils include white heather (*Cassiope tetragona*), yellow heather (*Phyllodoce glanduliflora*), arctic willow (*Salix arctica*), white mountain avens (*Dryas hookeriana*), bladder locoweed (*Oxytropis podocarpa*), sedges (*Carex* spp.), lichens, kruppelholz Engelmann spruce (*Picea engelmannii*) and kruppelholz alpine fir (*Abies lasiocarpa*) (Beder 1967).

The five ponds are located within 720 m of each other, at elevations between 2290 and 2330 m. All ponds were small (0.014 – 0.142 ha) and shallow (0.37 – 0.94 m). All five ponds lacked inflow streams. Only ER1 and ER3 had intermittent outflow streams that flowed during high water levels. Drainage basin size decreased from ER2 to SR2 to ER3 to ER1 to SFP. Pond bottoms consist of dark, highly organic and unconsolidated sediment with scattered rocks.

Climate

No long-term climate records are available for high elevation sites in the Canadian Rockies. The nearest long-term climate record is for Banff town site (1383 m above sea level; 51°11'N, 115° 34'W), 50 km south and 917 m lower than my study site (Figure 2.1; Environment Canada 2002). Mean annual air temperature for the last 100 years at Banff town site was 2.5 °C. Summer (June-September) air temperature was on average 12.1 °C but ranged from -1.4 °C to 26.6 °C. Of the last 100 years, the summer of 1998 was the 4th warmest (mean = 13.6 °C) and the summer of 1999 was the 11th coolest (mean = 11.0 °C) (Appendix 1). Mean annual precipitation for the last 100 years at Banff town site was 467 mm, with 267 mm as rain and 200 mm as snow. Half of the precipitation falls between May and August. Of the last 100 years, the year leading up to and including the ice-free season of 1998 (October 1997-September 1998) was the 27th driest (413 mm) and the year leading up to and including the ice-free season of 1999 (October 1998-September 1999) was the 37th wettest (495 mm) (Appendix 1). When considering both air temperature and precipitation, 1998 was the 3rd warmest and driest of the last 100 years

and 1999 was the 10th coolest and wettest in the last 100 years.

Sampling protocol and analyses

Four of the five ponds (ER1, ER2, ER3 and SR2) were sampled from May 24 to September 1, 1998 and all five ponds were sampled from June 10 to September 24, 1999.

Physical features

Air temperature and precipitation were monitored at the study site through the 1998 and 1999 ice-free seasons. Air temperature was measured in the shade one meter above the ground at one hour intervals by Onset Hobo® Temperature loggers. Precipitation was measured using an all-weather precipitation gauge that was emptied at least twice a week.

Water temperature was measured at mid-depth in each pond at one hour intervals by temperature loggers. Additional temperature loggers were placed in ER3 15 cm above the pond bottom and 15 cm below the water surface to document any thermal stratification. Temperature loggers were also placed in ER3 and SFP at the sediment-water interface at the deepest point during the winters of 1999/2000 and 2000/2001 to monitor pond temperatures through the winter. On March 20, 2001 an ice auger was used to core to the bottom of ER3 near the temperature logger to determine if liquid water was present.

Maximum water depth was recorded twice a week from a permanent water level gauge in each pond. Each pond was mapped using a compass, tape measure and permanent stakes along the shoreline. Surface area and volume were estimated using the bathymetric maps and the twice a week depth measurements.

Chemical features

Water was sampled by plunging two pre-rinsed 500 ml polyethylene bottles below the water surface at the center of each pond. Half of the water was filtered in the field through Whatman® GF/F filters. Water samples were stored in Camp Creek (< 6 °C) for up to two nights and then analyzed by the University of Alberta's Water Laboratory for ammonium (NH_4-N), nitrite plus nitrate (NO_2-N+NO_3-N), total phosphorus (TP), total

dissolved phosphorus (TDP), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), silica (Si), alkalinity (ALK) and pH every second week and chloride (Cl), sulfate (SO_4), sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg) monthly. Conductivity (COND) was measured twice a week *in situ* with a Cole-Parmer® handheld TDSTestr 40 with automatic temperature correction.

NH_4-N (unfiltered) and NO_2-N+NO_3–N (filtered) were determined colorimetrically with the Technicon™ Autoanalyzer™ II using automated berthelot and cadmium reaction, respectively. TP (unfiltered), TDP (filtered) (Prepas and Rigler 1982), SRP (filtered) (Murphy and Riley 1962) and soluble reactive Si (unfiltered) (Stainton et al. 1977) were determined colorimetrically with the Perkin Elmer 3300 Atomic Absorption Spectrometer. DOC (filtered) was measured on an Ionic Model 1505 Programmable Carbon Analyzer (APHA (American Public Health Association) 1992). Alkalinity (unfiltered) (ALK) was determined by acid titration with a Mettler DL21 Titrator (APHA 1992) and pH (unfiltered) was measured with a Fisher Scientific Accumet pH meter 925. Cl and SO_4 (filtered) were measured with the Dionex 2000i/SP Ion Chromatograph (EPA (Environmental Protection Agency) 1993). Na, K, Ca and Mg (filtered) were measured with the Perkin Elmer 3300 Atomic Absorption Spectrometer (Stainton et al. 1977).

Statistical Analysis

Univariate linear regression analysis was used to determine whether there was any functional relationship between air temperature and water temperature using JMP (SAS Institute 1996). Multiple linear regression analysis was used to examine the functional relationship between water loss and air temperature and total precipitation using JMP.

To determine the relative importance of evaporation and seepage in alpine pond water budgets, I used regression analysis to quantify slopes between water volume and chloride mass in each pond. I computed chloride mass by multiplying chloride concentration by pond volume on a given date. Chloride is considered to be conservative, therefore if chloride mass remain constant as pond volume decline then evaporation is likely the most important contribution to the loss of pond water. Conversely, if chloride mass decrease as

pond volumes decline then seepage is also an important contribution to the loss of pond water.

Two-tailed, t-tests were used to compare seasonal means between 1998 and 1999. If necessary, data were either $\log_{10}(x+1)$ or square root transformed to approximate normal distribution before statistical analysis (Zar 1999).

RESULTS

Climate

At the study site, mean air temperature was 3.8 °C warmer, minimum air temperature was 4.9 °C warmer, maximum air temperature was 1.7 °C warmer and daily air temperature ranges were 4.4 °C larger from June 15 to September 1 in 1998 than in 1999. In addition to having a shallower winter snowpack in the spring of 1998, total precipitation at the study site was 100 mm less from June 15 to September 1 in 1998 (160 mm) than in 1999 (260 mm).

Physical features

Freeze-thaw cycle

All four ponds dried in 1998 so I could not determine freeze-up dates nor monitor temperatures through the winter of 1998/1999. I therefore monitored temperatures through the winter of 2000/2001 in addition to 1999/2000. Ponds that did not dry during the 1999 and 2000 ice-free seasons, ER3 and SFP, started to freeze in late September. The timing of freeze-up varied between years depending on air temperature. For instance, air temperatures were cooler in 1999 than in 2000 (Figure 2.2) and consequently ER3 and SFP were ice-covered by October 9 in 1999 but not in 2000. Despite variability in the onset of freeze-up between years, temperatures at the sediment-water interface remained below freezing after October 30 in both 1999 and 2000 (Figure 2.2). Therefore in years with warm autumn air temperatures, the onset of freeze-up was delayed, but once air temperatures dropped below 0 °C, freezing to the sediment-water interface was rapid.

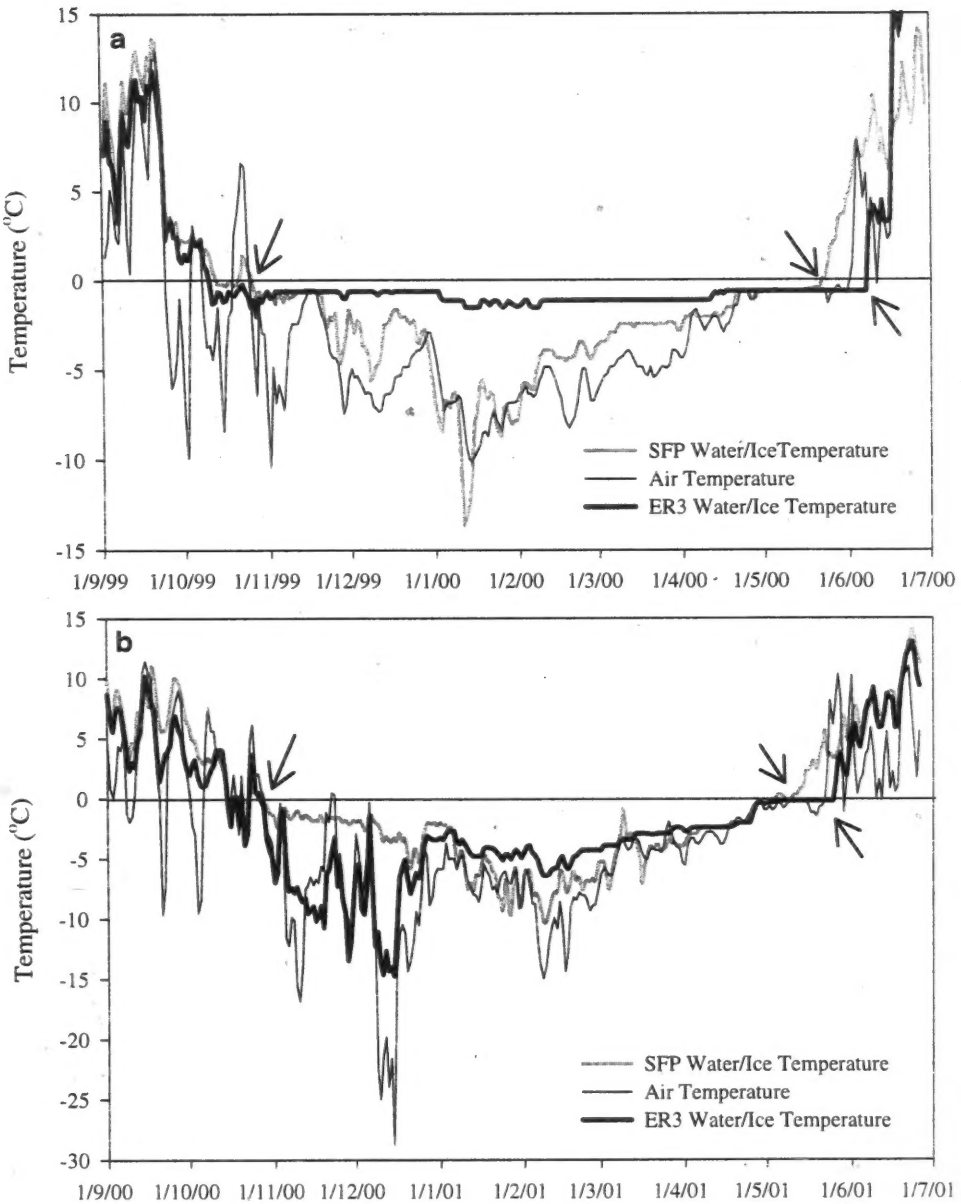


Figure 2.2: Daily mean air and water/ice temperature in alpine ponds East Ridge Three (ER3) and Snowflake Pond (SFP) from autumn to spring in 1999/2000 (a) and in 2000/2001 (b). Arrows mark when liquid water should be last and first present at the sediment-water interface. Air temperature was measured one meter above the ground in the shade. Water/ice temperatures were measured at the deepest point in the ponds at the sediment-water interface.

Temperatures at the sediment-water interface decreased to -14 °C during the winter (Figure 2.2). Freezing to the bottom was confirmed when no liquid water was found after coring to the bottom of ER3 on March 20, 2001.

Ice-out occurred in mid-May in 1998 and 2001 and in early June in 1999 and 2000. Timing of ice-out depended on snowpack depth and air temperatures. Ice-out occurred two weeks later in 2000, a year with above average snowpack and below average spring air temperatures (Environment Canada 2002), than in 2001 (Figure 2.2). Timing of ice-out for specific ponds also depended on the presence of snowdrifts on the ice, which affected albedo. For instance, ER3, which had a snowdrift covering its surface, retained surface ice cover for two weeks longer than SFP, which lacked a snowdrift (Figure 2.2). After ice-out, the sediments of the ponds remained frozen for up to two weeks.

Water temperature

Water temperatures below 1.5 °C were recorded on several dates during the summer in four of the ponds (Table 2.1; Figure 2.3). These low temperatures were associated with air temperatures < -0.6 °C and snow fall > 20 cm. The highest water temperature observed was 32.8 °C and water temperatures above 25 °C were recorded on several dates in all five ponds (Table 2.1; Figure 2.3). These high temperatures were associated with air temperatures > 20 °C and clear skies. Seasonal maximum water temperatures for each pond often occurred in the week prior to drying (Figure 2.3) when water volumes were low. Seasonal mean water temperatures were 1.5 to 2.4 °C warmer, seasonal minimum water temperatures were 1.6 to 2.2 °C warmer and seasonal maximum water temperatures were 0.4 to 3.7 °C warmer in 1998 than in 1999 (Table 2.1).

There were marked diurnal cycles in water temperatures (Figure 2.3). Daily water temperatures in the ice-free season fluctuated by 9.5 °C on average but varied by as little as 1.5 °C (5.8 to 7.3 °C) and as much as 23.6 °C (9.2 to 32.8 °C) (Table 2.1; Figure 2.3a and 2.3d). Daily water temperature closely followed air temperature (r^2 = 0.40 to 0.72, P < 0.0001) (Figure 2.3 and 2.4a). However, water temperatures typically reached higher daily maxima (1 to 5°C) than air temperatures (Figure 2.4a), suggesting that solar energy

Table 2.1: Mean (standard deviation), minimum and maximum values for physical features measured in the five alpine ponds in 1998 and 1999 in Banff National Park, Canada. Significant differences between 1998 and 1999 for each pond are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.001$).

	South Ridge Two		East Ridge One		East Ridge Two		East Ridge Three		Snowflake Pond
	1998	1999	1998	1999	1998	1999	1998	1999	1999
Air temperature (°C)	***8.7 (5.1)	6.7 (5.7)	***8.7 (5.1)	7.5 (5.8)	***9.9 (5.8)	7.2 (5.5)	***11.3 (6.3)	7.5 (5.8)	7.5 (5.8)
	-2.4-22.9	-7.3-22.9	-2.4-22.9	-7.3-26.3	-2.4-28	-7.3-22.9	-2.4-28.0	-7.3-26.3	-7.3-26.3
Water temperature (°C)	***12.7 (4.5)	10.9 (4.9)	***12.7 (4.5)	11.1 (5.3)	***12.9 (4.9)	11.4 (5.0)	***14.1 (4.6)	11.7 (3.8)	12.7 (4.2)
	1.1-24.7	1.2-27.5	0.3-23.8	0.6-29.9	0.3-32.8	0.3-27.5	1.4-27.5	2.6-22.9	3.1-25.0
Daily water	9.5 (4.3)	10.4 (4)	**9.1 (3.3)	11.0 (4.4)	10.0 (4.8)	11.3 (4.1)	***8.8 (4.2)	6.7 (2.7)	7.9 (3.2)
temperature range (°C)	2.9-22.0	2.1-18.1	3.5-18.7	1.6-22.5	3.0-23.6	3.1-19.7	2.0-20.2	1.5-12.8	2.2-16.1
Surface area (m^2)	87.7 (64.2)	94.3 (58.2)	**133.7 (79.0)	195.6 (50.2)	**124.9 (80.2)	179.2 (65.8)	439.2 (220.5)	513.5 (144.9)	1317.5 (331.2)
	0-138.8	0-138.8	0-213.0	0-213.0	0-215.7	0-215.7	0-574.3	82.9-574.3	12.7-1416.2
Volume (m^3)	16.6 (17.1)	16.8 (15.8)	**21.2 (25.9)	42.1 (20.6)	19.5 (22.6)	26.1 (15.9)	132.5 (91.6)	143.2 (62.5)	312.7 (153.4)
	0-35.7	0-39.9	0-65.7	0-65.7	0-55.2	0-54.3	0-281.4	9.9-245.8	31.4-546.7
Maximum depth (cm)	17.9 (15.2)	18.4 (13.5)	**15.0 (14.0)	26.6 (10.6)	16.6 (13.1)	21.3 (9.4)	58.7 (25.2)	64.8 (13.9)	37.2 (11.4)
	0-34.0	0-34.5	0-38.0	0-38.1	0-36.0	0-35.6	0-90.0	23.5-81.6	12.7-52.1

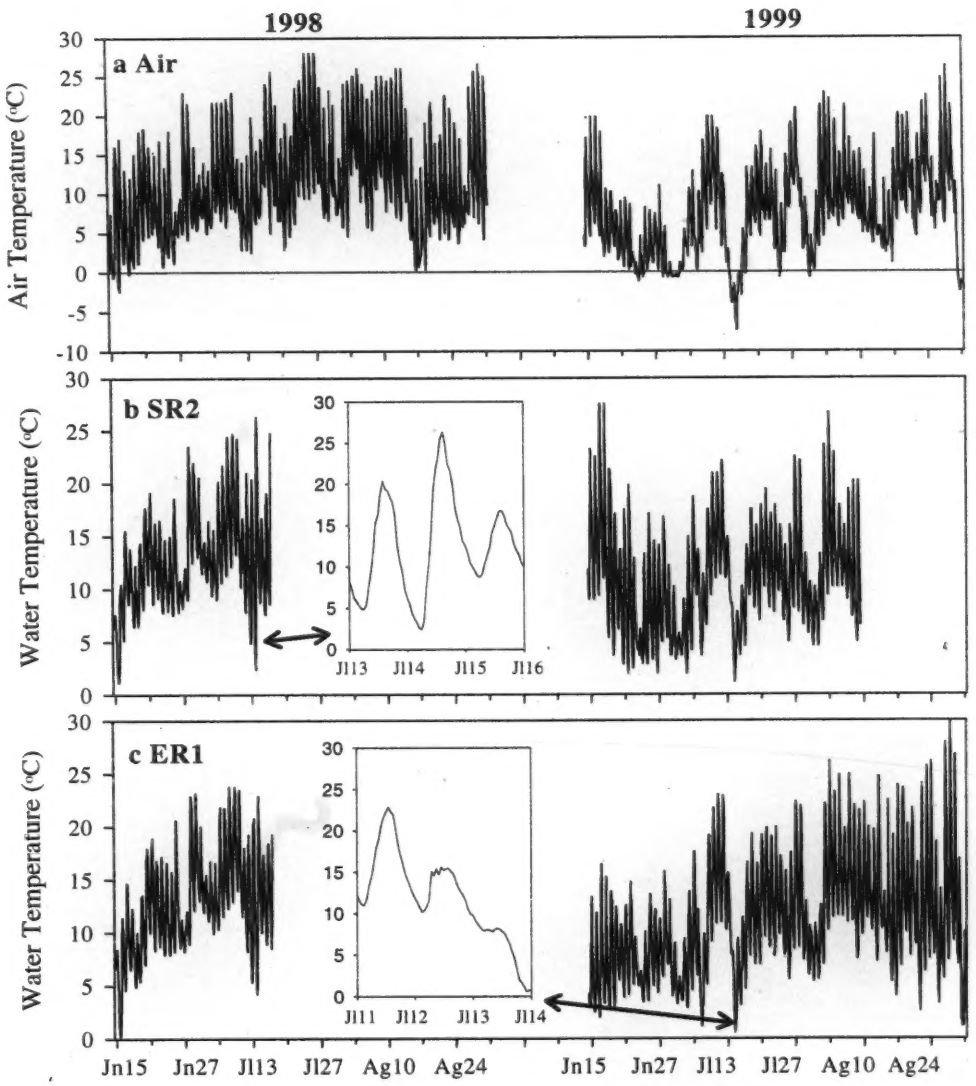


Figure 2.3a: Time series of air temperature (a) and water temperatures taken at mid-depth in South Ridge Two (b) and East Ridge One (c) in 1998 and 1999. Three daily temperature records are given in an insert for South Ridge Two (b) and East Ridge One (c). Regression equations for water temperature to air temperature are: WTempSR298 = 0.55ATemp98 + 7.85 $r^2 = 0.40$, $P < 0.001$; WTempSR299 = 0.71ATemp99 + 6.13 $r^2 = 0.67$, $P < 0.001$; WTempER198 = 0.71ATemp98 + 6.42 $r^2 = 0.65$, $P < 0.001$; and WTempER199 = 0.73ATemp99 + 5.57 $r^2 = 0.67$, $P < 0.001$.

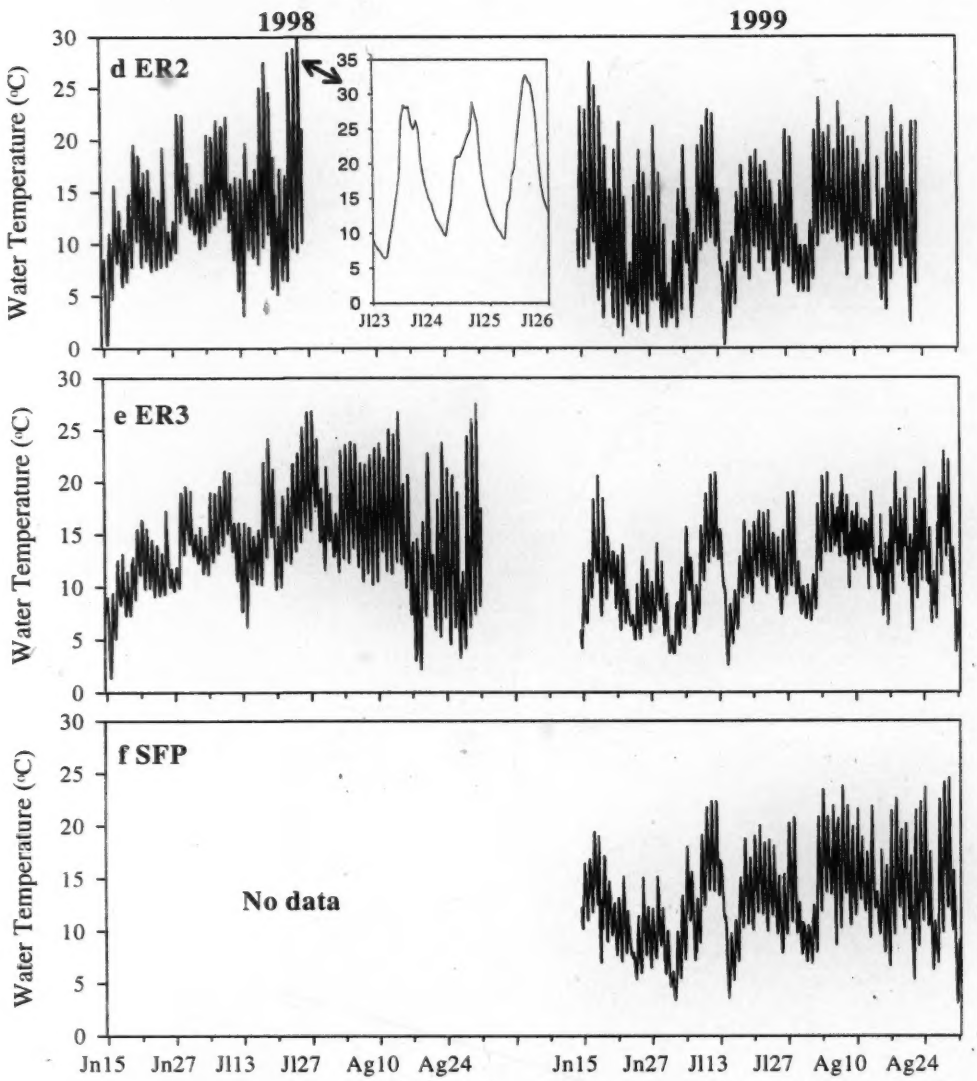


Figure 2.3b: Time series of water temperatures at mid-depth in East Ridge Two (d), East Ridge Three (e) and SnowflakePond (f) in 1998 and 1999. Three daily temperature records are given in an insert for East Ridge Two (d). Regression equations for water temperature to air temperature are: WTempER298 = 0.68ATemp98 + 6.17 r^2 = 0.65, P < 0.001; WTempER299 = 0.65ATemp99 + 6.14 r^2 = 0.65, P < 0.001; WTempER398 = 0.60ATemp98 + 7.43 r^2 = 0.64, P < 0.001; WTempER399 = 0.54ATemp99 + 7.60 r^2 = 0.68, P < 0.001; and WTempSFP99 = 0.61ATemp99 + 8.15 r^2 = 0.72, P < 0.001.

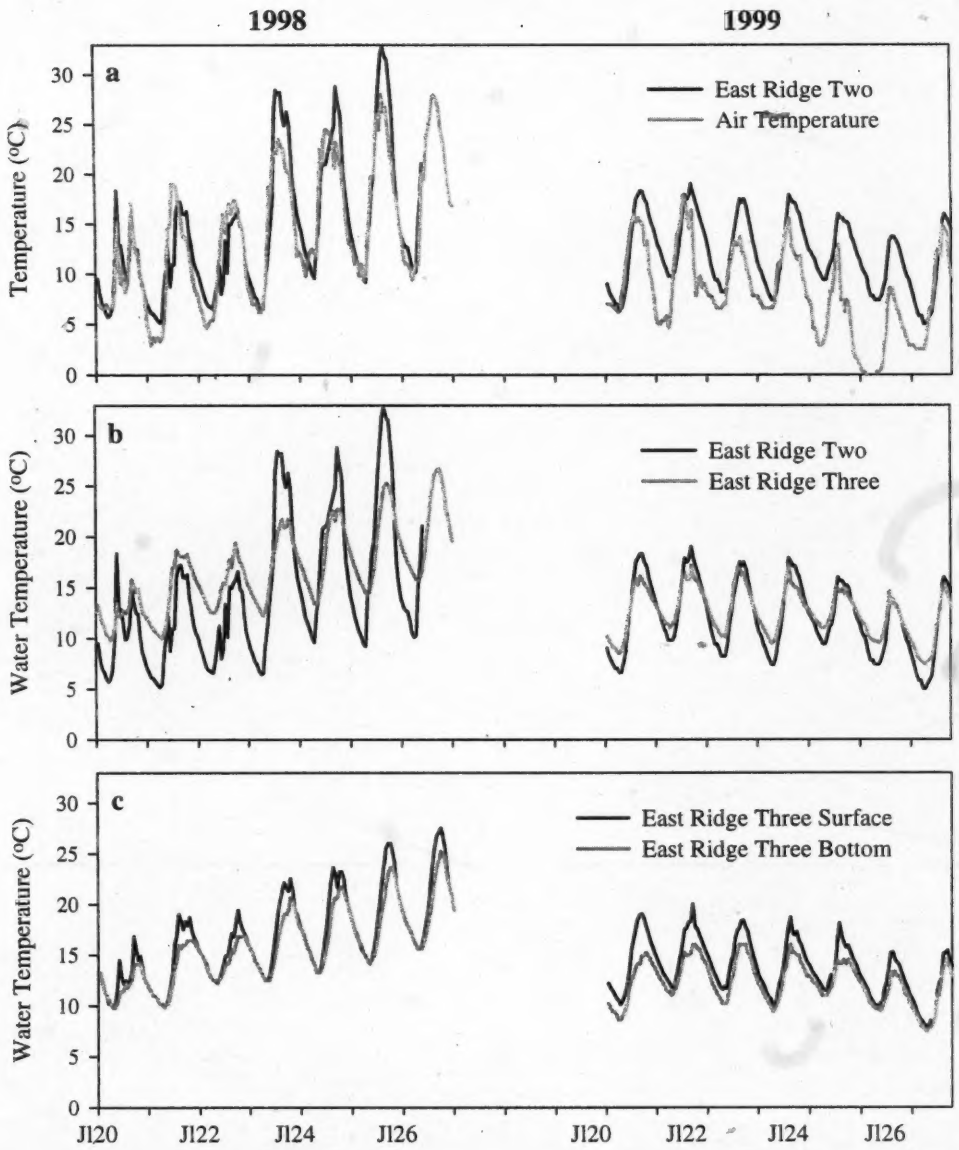


Figure 2.4: Time series of air temperatures and water temperatures taken at mid-depth in East Ridge Two demonstrating the how close water temperature followed air temperature (a); water temperatures taken at mid-depth in East Ridge Two and Three demonstrating the difference in temperature between shallow and deep ponds (b); and water temperatures taken 15 cm below the surface and 15 cm above the bottom in East Ridge Three demonstrating minimal thermal stratification (c).

absorption is an important heat source in these ponds. On any give day, small, shallow ponds (SR2, ER1 and ER2) had greater daily minima and maxima than large, deep ponds (ER3 and SFP) (Figure 2.4b). Daily water temperature ranges in ER3 were significantly greater in 1998 than in 1999 (Table 2.1). However daily water temperature ranges in SR1, ER1 and ER2 were greater in 1999 than in 1998 (Table 2.1) because I missed temperature measurements just before these ponds dried in 1998.

Alpine ponds had minimal thermal stratification (Figure 2.4c). Surface and bottom temperatures were typically within 1 °C. However, when water temperatures reached their daily maximum, surface and bottom temperatures differed by 1 to 4 °C (Figure 2.4c).

Water budget

Water volumes, surface areas and maximum depths were seasonally variable (Table 2.1). In 1998, maximum water volumes occurred at or just after ice-out and volumes declined continuously through the ice-free season (Figure 2.5). All four ponds were dry by September 4, 1998. In 1999, water volumes were more variable and increased several times during the ice-free season (Figure 2.5). In 1999, maximum water volumes in four of the ponds occurred in early July after three days of cold temperatures and snow (Figure 2.5). SR2, ER1 and ER2 were dry by early September 10, 1999. SR2 dried 16 days earlier in 1998 than in 1999 and ER1 and ER2 dried 29 days earlier in 1998 than in 1999. ER3 and SFP did not dry during the ice-free season in 1999. Seasonal mean surface areas, volumes and maximum depths were lower in 1998 than in 1999 (Table 2.1).

Water volumes decreased most rapidly during warm-dry periods and increased only after precipitation events (Figure 2.5). However in 1998, air temperature and precipitation explained little of the variation in water volumes (Water loss = - 0.02 – 0.27$\log_{10}$(Mean Precipitation +1) + 0.07Mean Temperature; $r^2 = 0.02$; $P = 0.70$). In 1999, air temperature and precipitation collectively explained 20% of the variation in water volumes (Water loss = 0.10 - 2.83$\log_{10}$(Mean Precipitation+1) + 0.36Mean Temperature; $r^2 = 0.20$; $P < 0.0001$). These weak relationships between water volume loss, air temperature and

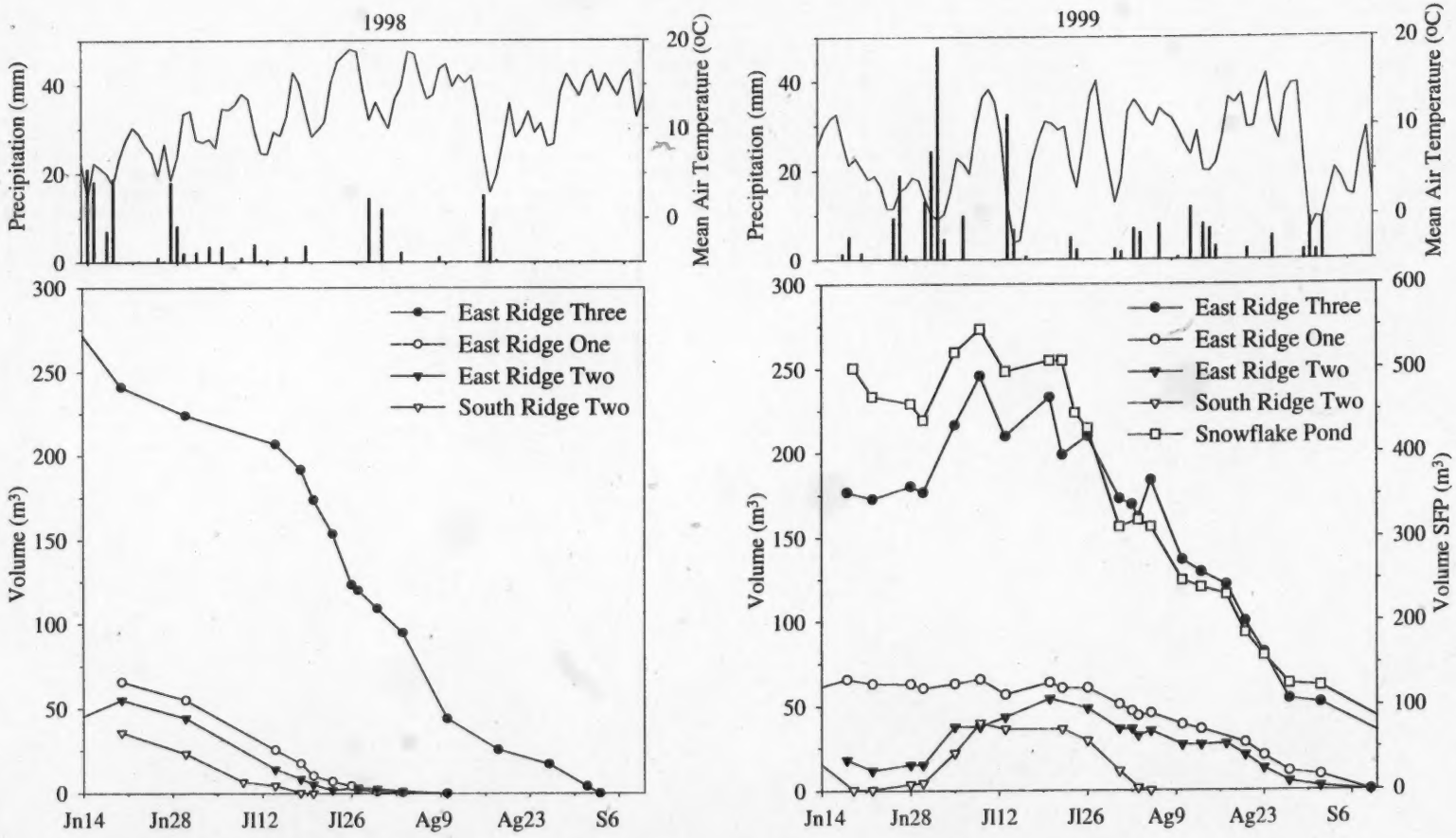


Figure 2.5: Daily precipitation (bar graph), daily mean air temperature (solid line) and volume of the five alpine ponds studied during the 1998 (left) and 1999 (right) ice-free seasons.

precipitation suggest alpine pond water budgets are controlled by more than just atmospheric inputs and outputs. Seepage is likely an important source of water loss from some ponds based on the positive relationship between chloride mass within the basin and water volume (Table 2.2).

Table 2.2: Slope for chloride mass versus water volume (m^3) for each alpine pond during the ice-free seasons of 1998 and 1999. If seepage was also an important source of water loss, chloride mass within a basin would decrease as water volumes decline and there would be a significant positive slope. Slopes significantly different from zero are indicated (* = $P < 0.1$, ** = $P < 0.05$).

Pond	Year	Chloride Mass (g/basin)
South Ridge Two	1998	n = 2
South Ridge Two	1999	0.505
East Ridge One	1998	n = 2
East Ridge One	1999	0.430
East Ridge Two	1998	-0.105
East Ridge Two	1999	**0.540
East Ridge Three	1998	0.274
East Ridge Three	1999	**0.380
Snowflake Pond	1999	*0.367

Chemical variables

Alkalinity, pH, conductivity and major ions

These alpine ponds were dilute (mean conductivity 61.9 µS cm^{-1}) and poorly buffered (mean alkalinity 0.55 meq L^{-1}) yet were fairly neutral (mean pH = 7.2). The dominant major ions were bicarbonate, magnesium and calcium. The general trend in relative concentrations of cations was Mg>Ca>Na>K, with means of 0.293, 0.266, 0.030 and 0.012 meq L^{-1}, respectively and of anions was HCO_3>Cl>SO_4 with means of 0.54, 0.038 and 0.007 meq L^{-1}, respectively (Appendix 2). In general, alkalinity, pH, conductivity and ion concentrations were higher and more variable in ER1 and SFP than in SR2, ER2 and ER3 (Figure 2.6 and 2.7). Alkalinity, pH, conductivity, HCO_3, Mg and Ca concentrations were lowest at ice-out and increased over the summer (Figure 2.6 and 2.7). Of the remaining ions, only SO_4 in ER1 in 1999 showed a consistent increasing seasonal trend (Figure 2.7).

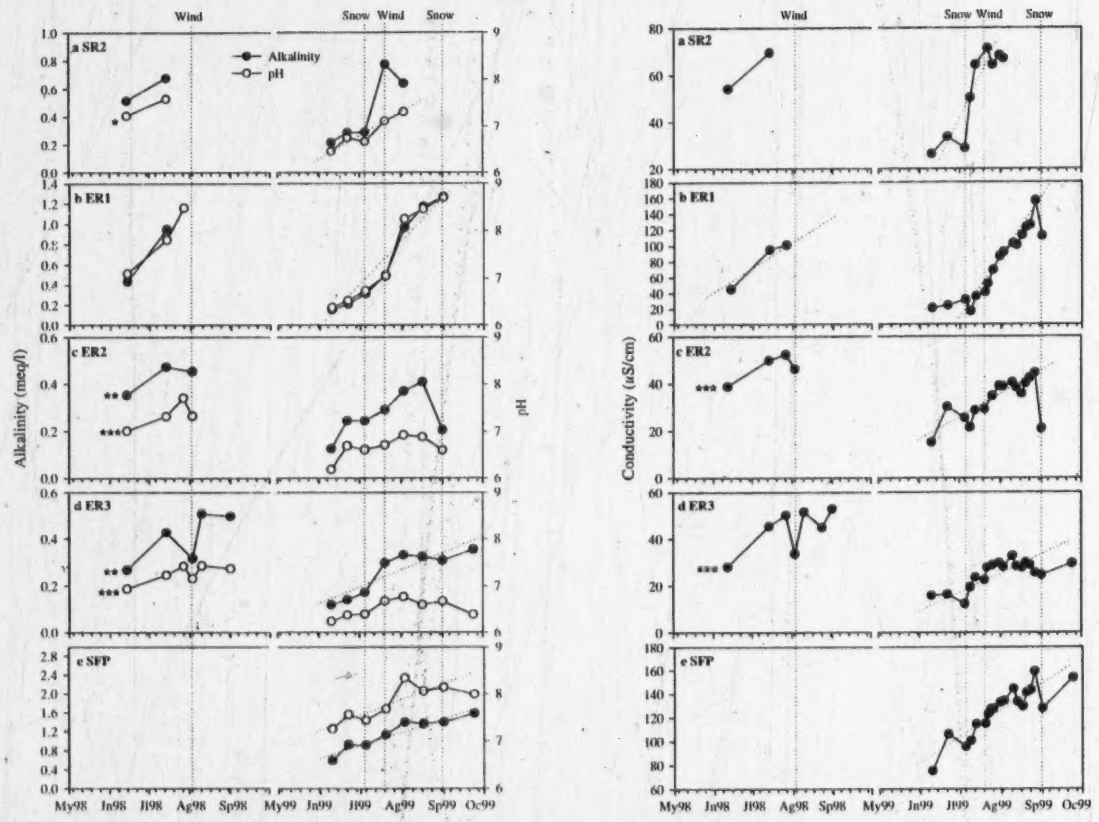


Figure 2.6: Time series of alkalinity, pH and conductivity measured in South Ridge Two (a), East Ridge One (b), East Ridge Two (c), East Ridge Three (d) and Snowflake Pond (e) during the 1998 and 1999 ice-free seasons. Seasonal trends shown by dotted lines are significantly different from zero. Significant differences between the 1998 and 1999 means are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.001$). Samples taken after windstorms and snowstorms are labeled.

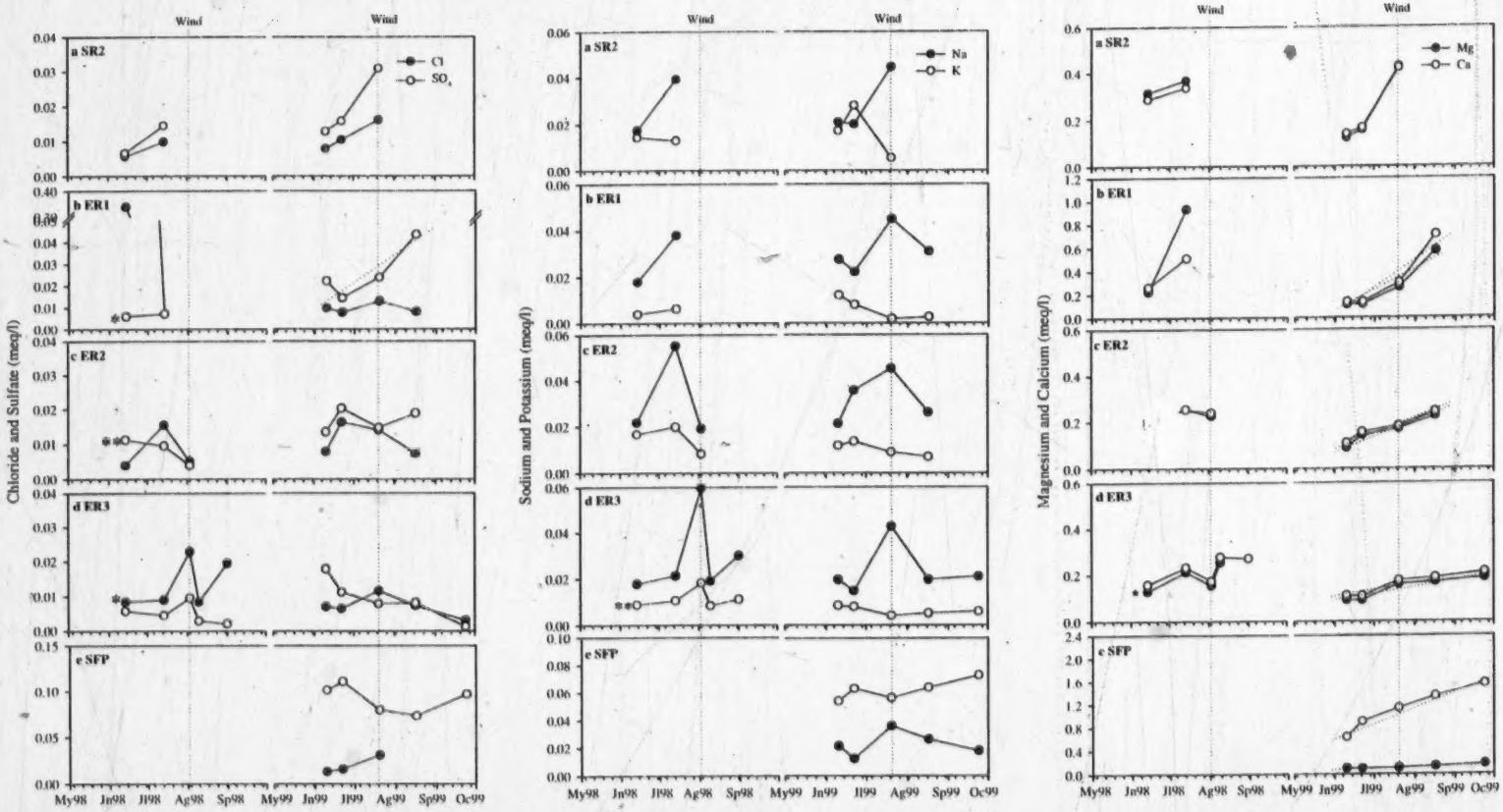


Figure 2.7: Time series of major ion strength measured in South Ridge Two (a), East Ridge One (b), East Ridge Two (c), East Ridge Three (d) and Snowflake Pond (e) during the 1998 and 1999 ice-free seasons. Seasonal trends shown by dotted lines are significantly different from zero. Significant differences between the 1998 and 1999 means for each ion are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.001$). Samples taken after windstorms are labeled.

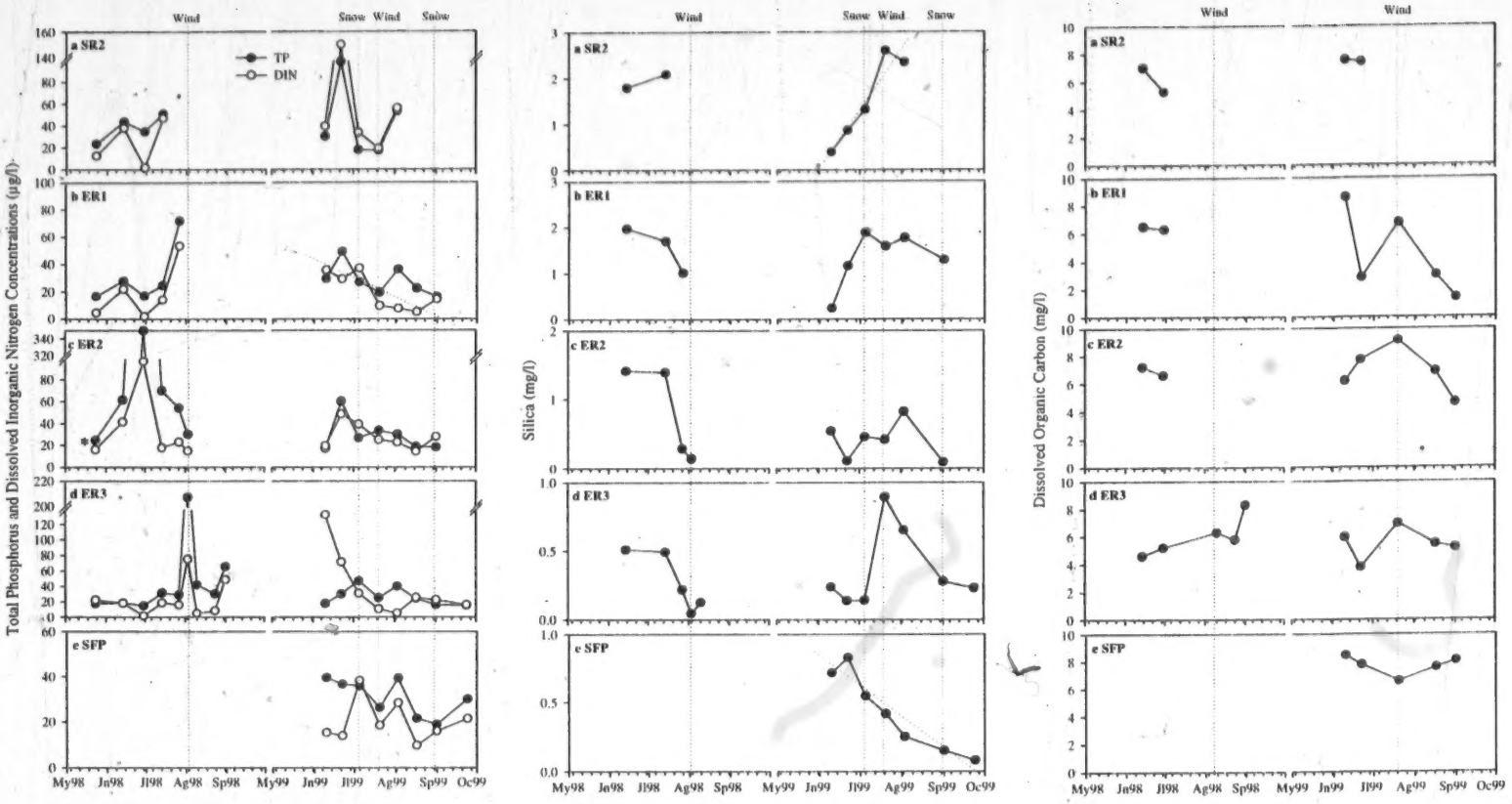


Figure 2.8: Time series of nutrient concentrations measured South Ridge Two (a), East Ridge One (b), East Ridge Two (c), East Ridge Three (d) and Snowflake Pond (e) during the 1998 and 1999 ice-free seasons. Seasonal trends shown by dotted lines are significantly different from zero. Significant differences between the 1998 and 1999 means for each nutrient are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.001$). Samples taken after windstorms and snowstorms are labeled.

After a windstorm on August 3, 1998 alkalinity, pH, conductivity, Ca and Mg decreased and Cl, SO_4, Na and K increased in ER3 (Figure 2.6 and 2.7). A windstorm on July 20, 1999 did not drastically change alkalinity, pH, or conductivity (Figure 2.6) but Cl, Na, Mg and Ca generally increased and SO_4 and K generally decreased (Figure 2.7). After snowstorms in early July and late August 1999, alkalinity, pH and conductivity decreased in SR2, ER2, ER3 and SFP, with the exception of pH in ER3 and SFP in late August (Figure 2.6).

Alkalinity, pH and conductivity in ER2 and alkalinity, pH and conductivity, Cl, K and Mg in ER3 were higher in 1998 than in 1999 (Figure 2.6 and 2.7). SO_4 in ER 1 and ER2 was lower in 1998 than in 1999 (Figure 2.7).

Nutrients

DIN and TP concentrations were always above detection limits in alpine ponds (Figure 2.8). NH_4-N (mean = 20.9 $\mu g\ L^{-1}$) was higher than NO_2-N+NO_3-N (mean = 8.6 $\mu g\ L^{-1}$) (Appendix 2). Much of the TP (mean = 37.0 $\mu g\ L^{-1}$) was present as TDP (mean = 21.2 $\mu g\ L^{-1}$) and a smaller amount was present as SRP (mean = 6.3 $\mu g\ L^{-1}$) (Appendix 2). Mean Si concentration was 0.81 mg L^{-1} and mean DOC concentration was 6.6 mg L^{-1} (Appendix 2 and Figure 2.8). N, P and DOC concentrations were similar in all five ponds and silica concentrations were higher in SR2 and ER1 than in ER2, ER3 and SFP (Figure 2.8). DIN and TP concentrations showed no clear seasonal trends, except for a decreasing seasonal trend of DIN in ER1 in 1999 (Figure 2.8). Through the 1999 ice-free season, silica concentrations increased in SR2, decreased in SFP and showed no clear seasonal trend in the other three ponds (Figure 2.8). DOC concentrations showed no clear seasonal trend in any of the five ponds (Figure 2.8).

After a windstorm in August 3, 1998, DIN and TP concentrations increased > 4-fold in ER3 and silica concentrations slightly decreased in ER2 and ER3 (Figure 2.8). After a windstorm on July 20, 1999, DIN and TP concentrations showed no consistent response; DOC concentrations increased in ER1, ER2 and ER3 but decreased in SFP; and silica concentrations increased in SR2 and ER3, but slightly decreased in ER1, ER2 and SFP

(Figure 2.8). In 1999, Si concentrations increased in SR2, ER1 and ER2 and decreased in SFP after the early July snowstorm but decreased in all ponds after the late August snowstorm (Figure 2.8). N and P concentrations showed no consistent response to the snowstorms in early July and late August.

TP in ER2 was higher in 1998 than in 1999 but neither N nor P concentrations differed from 1998 and 1999 in any of the other ponds (Figure 2.8). Silica and DOC concentrations were similar in 1998 and 1999 (Figure 2.8).

DISCUSSION

Physical limnology of alpine ponds

These alpine ponds differ from low elevation prairie and arctic ponds in that they have large daily temperature ranges (DTR). The maximum DTR of 23.6 °C in these alpine ponds was much higher than the 12 °C range recorded in Canadian arctic (Miller et al. 1980) and prairie ponds (Daborn and Clifford 1974; Daborn 1976a) (Table 2.3). DTRs were not previously documented in North American alpine ponds but a DTR of 23.5 °C was measured in alpine ponds in the eastern Alps (Pichler 1939). Alpine ponds likely have large DTR because the alpine has high insolation and consequently alpine ponds warm considerably during the day. In addition, the alpine has low insulation and high thermal radiation and consequently alpine ponds cool considerably during the night. Arctic ponds lack large DTR because and the low sun angle results in low insolation and therefore cool air temperatures and minimal solar energy absorption (Miller et al. 1980). In contrast, solar energy absorption was inferred to be an important heat source in these study ponds.

The warmest water temperature of 32.8 °C recorded in these alpine ponds was warmer than recorded in other alpine (Pichler 1939; Schmitz 1959) and arctic ponds (Miller et al. 1980; Douglas and Smol 1994) (Table 2.3). Southern aquatic systems may reach temperatures as high as those seen in these alpine ponds, but do not generally get as cool at night (Black 1976). Although the effect of these warm daily temperature maxima and large DTR on biological communities is unknown, temperature has an overriding

Table 2.3: Physical and chemical features found in these alpine ponds, other alpine ponds, arctic ponds and northern prairie ponds. References and locations for the data are given below.

Feature	These alpine ponds	Other alpine Ponds[1,2,3]	Arctic ponds[4,5]	Northern prairie ponds[6,7]
Daily temperature ranges	<23.6 °C	<23.5 °C [1]	<12 °C [4]	<12 °C [6,7]
Ice-free season maximum temperature	32.8 °C	30.0 °C [1] 19.8 °C [3]	20 °C [4] 18 °C [5]	23 °C [6] 25 °C [7]
Ice-free season minimum temperature	0.3 °C	7.0 °C [3]	0.5 °C [4] 1.0 °C [5]	5.0 °C [6] 0.5 °C [7]
Maximum thermal stratification	0-4 °C	1-4 °C [3]	0.5 °C [4]	< 0.5 °C [7]
Aestival (freeze to the bottom)	Yes	Yes [2.3]	Yes [4.5]	Yes [6]
Bottom ice after thaw	Yes	Yes [2]	Yes [4]	Yes [6]
Length of ice-free season	<150 days	90-120 days [2]	60-90 days [4] 42-49 days [5]	240 days [6]
Seasonally variable water levels	Yes (<82 cm)	Not recorded	Yes (<16 cm) [4]	Yes (<47 cm) [6] Yes (<30 cm) [7]
Seasonal desiccation	Some	Not recorded	Not recorded	Some

Alpine: **1.** Pichler 1939 (Eastern Alps); **2.** Neldner and Pennak 1955 (3507m, Rocky Mountain National Park, Colorado); and **3.** Schmitz 1959 (3582m, Loveland Pass, Colorado). Arctic: **4**. Hobbie 1980 (Barrow, Alaska) and **5.** Douglas and Smol 1994 (Cape Herschel, Nunavut). Prairie: **6.** Daborn and Clifford 1974 (Edmonton, Alberta) and **7.** Daborn 1976a (Edmonton, Alberta).

importance on nearly all functions within an ecosystem because of its effect on the rate of biochemical reactions. Temperature affects algal community productivity, biomass and composition (DeNicola 1996) and invertebrate feeding rates, growth, size, biomass and composition (Hogg et al. 1995; Moore et al. 1996). Temperature also affects the biological community indirectly through modification of the chemical environment (Sommaruga-Wögraph et al. 1997).

Although the large DTR may make alpine ponds one of the most physically variable aquatic environments on earth, there are additional physical and chemical features shared among alpine, arctic and other northern ponds that make them particularly demanding ecosystems. These include: impact of severe weather events, lack of thermal stratification, freezing solid in the winter and fluctuating water volumes.

Similar to prairie ponds, summer snowstorms resulted in dramatic declines in alpine pond water temperatures (Daborn 1976b) (Table 2.3). Water temperatures close to 0 °C were also recorded in arctic ponds when air temperatures declined below freezing (Douglas and Smol 1994). The alpine is more likely to have large mid-summer snow events and the resulting low water temperatures than either the prairies or the arctic. Summer snowstorms and declining temperatures affected the water chemistry (discussed below) and likely impacted the biological community in these alpine ponds. In a prairie pond, large fairy shrimp (*Eubranchipus bundyi*) died when water temperatures fell to 0.5 °C after an early summer snowstorm (Daborn 1976b).

Similar to other northern ponds (Daborn 1976a; Miller et al. 1980), development of thermal stratification in alpine ponds study here is likely constrained by strong winds, lack of trees, high water transparency and cold nights. High water transparency allows solar radiation to penetrate to the bottom and warm not only the water but also the sediment, which then warms the water from below, creating convection currents. Thermal radiation from the water surface during the night likely cools the surface water, again creating convection currents. The lack of thermal stratification and therefore thermal refuge for pond organisms is of particular concern given the observed extreme minimum

and maximum water temperatures and the large DTR. Further research is needed on the chemical and biological effects of large DTR and extreme minimum and maximum water temperatures in systems with limited thermal stratification, such as alpine ponds.

Alpine ponds studied here are classified as aestival because temperatures at the sediment-water interface decreased well below freezing during the winter. Liquid water was absent and sediment was frozen in March. Aestival ponds are abundant at high altitudes (Neldner and Pennak 1955) and latitudes (Daborn and Clifford 1974; Miller et al. 1980) where air temperatures remain significantly below zero for several months (Table 2.3). Aestival ponds provide unique physical and chemical conditions during freezing and thawing. As a pond freezes, cryoconcentration of particulate and dissolved matter occurs (Daborn and Clifford 1974). These concentrated solutes and particulates are forced into the sediment when the pond freezes solid (Prentki et al. 1980). Resident organisms must either have the ability to migrate to a suitable overwintering habitat or mechanisms to avoid (e.g. resting stage, super cooling, ancillary structures and thermal hysteresis) or tolerate freezing (cryroprotectors) (Daborn 1974; Danks 2000). As the ponds thaw, most of the organisms and particulate and dissolved matter from the previous ice-free season remain within the frozen sediment (Daborn and Clifford 1974). Organisms likely thaw quickly once the ice has melted (Danks 2000) and chemical re-solution from the sediment occurs throughout the summer (Prentki et al. 1980).

The ice-free season in these alpine ponds is longer than in arctic ponds (Miller et al. 1980) but shorter than in northern prairie ponds (Daborn and Clifford 1974) that have been studied (Table 2.3). The length of the ice-free season in these alpine ponds is similar to nearby alpine lakes, but the ponds thaw and freeze one month earlier than the lakes. I also observed alpine ponds located in mountain shadows with large permanent snowpacks that had much shorter ice-free seasons than the five study ponds. Although such ponds are not abundant, they likely have different physical and chemical features than the ponds I studied.

Consistent with other ponds worldwide (Hartland-Rowe 1972; Daborn 1974; Hobbie

1980; Williams 1996), water budgets of these alpine ponds were unbalanced and water volumes fluctuated considerably, often leading to complete desiccation by mid- to late-summer. Precipitation, particularly winter snowpack, is the main water input to these alpine ponds. Similar to arctic ponds (Miller et al. 1980), depth of the winter snowpack and rate of snowmelt controls the water volume in alpine ponds early in the ice-free season. During snowmelt, soils are still frozen and impermeable to infiltration so the majority of the snow in the basin enters the pond. Summer precipitation had only a minor influence on the water volumes except when air temperatures were cold and precipitation fell in numerous repeated events, or as heavy snow. Unlike most arctic and low elevation ponds which have been studied (Miller et al. 1980; Covich et al. 1997), seepage was likely more important than evaporation as the main water output from some the alpine ponds I studied.

Chemical limnology of alpine ponds

Ionic chemistry in these alpine ponds is controlled primarily by precipitation and seepage, whereas evaporation is more important than precipitation and seepage in arctic ponds in Alaska (Prentki et al. 1980). In arctic ponds, evaporation leads to concentration of dissolved salts over time and consequently mean ion concentrations, alkalinity and conductivity were higher in arctic ponds than in alpine ponds I studied (Prentki et al. 1980; Douglas and Smol 1994). Evaporation also leads to seasonal increases in ion concentrations, alkalinity and conductivity in arctic ponds in Alaska and Nunavut (Prentki et al. 1980; Douglas and Smol 1994). However, in these alpine ponds, ion concentrations did not consistently increase through the ice-free season. Although the three dominant ions (HCO_3, Ca and Mg) and consequently alkalinity and conductivity increased during the ice-free season, these increases were typically weakly correlated with water volume loss.

Some of the seasonal trends in ion concentrations can be explained by dilution by precipitation (all ions < 0.5 mg L^{-1}; conductivity < 10 µS cm^{-1}; alkalinity < 0.40 meg L^{-1}) depending on drainage basin size. Ion concentrations in ponds were typically low early in the ice-free season after the majority of the winter snowpack melted. Dilution by

precipitation also occurred after summer snowstorms in most ponds. However, dilution by precipitation was not as important in ponds with larger drainage basins. For instance, ER1 and SFP generally had higher ion concentrations, alkalinity and conductivity after snowmelt than ponds with smaller drainage basins. Furthermore, alkalinity in ER1 and SFP usually increased rather than decreased after summer snowstorms. These contrast with results from the arctic where precipitation had a greater dilution effect in ponds with large drainage basins (Douglas and Smol 1994). This difference likely is due to alpine soils having deeper mineralization zones and less permafrost than arctic soils therefore runoff is richer in dissolved solutes from the larger drainage basins in the alpine.

In northern prairie and arctic ponds, seasonal increases in ion concentrations were also linked to re-solution of ions concentrated in the sediment during the previous year (Daborn 1976a; Prentki et al. 1980). However in alpine ponds I studied the importance of re-solution from the sediment appears to be less important, because during the summer not all ions increased when the sediment melted or was disturbed by windstorms.

Dissolved reactive silica concentrations in these alpine ponds were similar to arctic ponds (Prentki et al. 1980). Low concentrations (< 0.5 mg L^{-1}) usually cause silica limitation in diatoms and other siliceous algal species. In arctic ponds, planktonic diatoms are absent and benthic diatoms keep silica concentrations in the water column fairly constant through the ice-free season (Douglas 1989). Similarly, diatom uptake of silica in these alpine ponds likely influenced seasonal patterns in dissolved reactive silica and may have obscured the impacts of precipitation and sediment disturbance.

DOC concentrations in these alpine ponds were ten times higher than nearby alpine lakes. Higher concentrations were likely due to ponds having more heavily vegetated drainage basins and therefore more allochthonous DOC inputs. Furthermore, ponds have higher bottom surface area to water volume ratios and consequently more autochthonous DOC than alpine lakes. The significance of sediments as a carbon source in alpine ponds was shown when DOC concentrations increased after a windstorm disturbed bottom sediments.

DOC is of particular interest because of its ability to attenuate biologically damaging ultraviolet radiation (UVR) (Scully and Lean 1994). Biological damage due to UVR increases markedly when DOC concentrations drop < 2-3 mg L^{-1} in low elevation lakes (Scully and Lean 1994). However DOC quality, in addition to DOC quantity, influences its UVR attenuation capability. Consequently, even though DOC concentrations in alpine ponds were > 3 mg L^{-1}, DOC quality in alpine ponds likely has a larger autochthonous component than low elevation systems. Therefore DOC in mountain lakes and ponds absorbs less incident radiation and allows deeper UVR penetration (McKnight et al. 2001). For instance, in montane lakes a high percentage of UVR penetrated below 50 cm when DOC concentrations were between 7-10 mg L^{-1} (Tank 2002). Given the shallow depth of alpine ponds, a high percent of incident UVR likely penetrates to their sediments.

Nitrogen and phosphorus concentrations in these alpine ponds were similar to those arctic ponds (Prentki et al. 1980; Douglas and Smol 1994). High nutrient concentrations in alpine ponds reflect precipitation rich in NH_4-N (> 40 µg L^{-1}); runoff from the N-limited terrestrial ecosystem likely rich in P and poor in N (Bowman et al. 1993; Campbell et al. 2000); and sediments likely rich in nutrients. Sediments are likely an important nutrient source in alpine ponds similar to arctic ponds and shallow lakes (Prentki et al. 1980; Alexander et al. 1989; Scheffer 1998). However, nutrient concentrations in these alpine ponds did not always increase after windstorms disturbed the sediments. This may reflect rapid *in situ* abiotic (e.g. absorption to organics and inorganics and sedimentation) and biotic (e.g. algal uptake and bacterial nitrification and denitrification) controls that quickly decrease nutrient concentrations after sediment disturbance. These *in situ* controls may also explain why nutrient concentrations did not change significantly after snowstorms.

Nutrient limitation in mountain lakes is accurately predicted by the water column DIN:TP ratio (by weight) (Morris and Lewis 1988; Sickman 2001). If DIN:TP ratio is less than one, N-limitation is indicated and greater than four, P-limitation is indicated. A ratio between one and four indicates intermediate limitation, i.e. reciprocal or co-limitation by

either N or P. DIN:TP ratios in these alpine ponds imply general N-limitation. Intermediate limitation was common early in the ice-free season and after summer snowstorms because precipitation had a high DIN:TP ratio (> 6). Although nearby Snowflake Lake is P-limited (Paul et al. 1995), N-limitation has been well documented in subalpine and alpine lakes throughout the western United States (Morris and Lewis 1988; Sickman 2001; Lafrançois 2002). A general tendency towards N-limitation makes alpine aquatic ecosystems particularly susceptible to current increases in atmospheric N deposition (Baron et al. 2000).

Comparison of alpine and arctic ponds

Many aspects of alpine ponds I studied are similar to those observed in arctic ponds studied in Barrow, Alaska (Prentki et al. 1980) and Cape Herschel, Nunavut (Douglas and Smol 1994) such as a lack of thermal stratification, freezing solid in the winter and periods of very cold-water temperatures observed during the summer. In addition, both alpine and arctic ponds have dynamic water budgets that are mainly controlled by snow and precipitation. However, seepage in addition to evaporation is an important water output in these alpine ponds. Alpine ponds have larger daily temperature ranges, warmer seasonal maxima and longer ice-free seasons than arctic ponds. Chemically, these alpine ponds are more dilute in ions and have lower alkalinities than arctic ponds (Prentki et al. 1980; Douglas and Smol 1994). Despite these dissimilarities, both alpine and arctic ponds (Douglas and Smol 1999) are likely sensitive to climate change and their physical environments may become even more demanding as the climate changes.

Climate change and alpine pond physical limnology

Warmer water temperatures were one of the most consistent responses in these alpine ponds to the warm-dry year. Warmer water temperatures are a common response to climate warming in lakes, streams and rivers (Webb 1996; Schindler 1997). For example, boreal lakes warmed by approximately 0.6 °C for every degree of air temperature warming (Schindler 1997). In these alpine ponds, water temperatures warmed by 0.55 – 0.73 °C for every degree of air temperature warming, with small, shallow ponds warming

the most. As reviewed above, the biological implications of these warmer temperatures are numerous (Hogg et al. 1995; Moore et al. 1996; DeNicola 1996).

I also observed more extremely warm temperature events and fewer summer snowstorms during the warm-dry year. The ecological impact of these brief but extreme events in alpine ponds is unknown but should be significant, especially because ponds lack a thermal refuge. It has been suggested that many of the gradual long-term biotic changes seen in terrestrial communities are a result of a few, brief, extreme events rather than a gradual shift in the mean (Easterling et al. 2000; Parmesan et al. 2000). The significance of brief, extreme events in aquatic ecosystems needs further study, especially since extreme events are expected to increase in the future in response to climate change (Meehl et al. 2000).

All four alpine ponds were ice free over three weeks earlier during the warm-dry year. Similarly, lakes and rivers in the Northern Hemisphere have become ice free progressively earlier in the last century (Magnuson et al. 2000). Earlier ice-free seasons corresponded to warmer spring air temperatures and shallower snowpacks in both alpine ponds and other aquatic systems (Robertson 1989). The potential physical, chemical and biological implications of earlier ice off are numerous (Schindler 1997). Early ice off makes alpine ponds susceptible to late spring snowstorms and the resulting extremes in physical and chemical conditions (low temperatures, increased water levels and chemical dilution). Earlier ice off can increase degree-days which may allow invasion of new species previously limited by degree-days (Lamontagne et al. 1994). The most notable impact of early thaw in these alpine ponds was the longer ice-free season, which may increase the chance of permanent ponds drying and temporary ponds drying earlier.

Three of the alpine ponds studied here dried 16-29 days earlier during the warm-dry year. The largest and deepest pond only dried in the warm-dry year, when water input was less from the winter snowpack and summer precipitation. Evaporative water loss also likely increased, because air temperatures were higher and humidity lower in the warm-dry year. Periodic drying is already an important feature that shapes pond community ecology

(Wellborn et al. 1996). Decreased water volume, surface area and maximum depth and increased temperature and light are important, as well as complete drying. Although communities in ponds that historically dry are more resilient when faced with these physical changes, deviation from the typical drying regime may cause drastic ecological modifications (Havens 1994). Communities in ponds that rarely dry should show an even higher sensitivity to physical changes associated with drying than ponds that regularly dry.

Climate change and alpine pond chemical limnology

In contrast to physical features, the chemistry of alpine ponds I studied differed only slightly between warm-dry and cold-wet years. The chemistry of SR2 and ER1 changed slightly, whereas the chemistry of ER2 and ER3 changed moderately. Much of the chemical response in ER2 and ER3 to warm, dry conditions was similar to the response in nearby alpine lakes and in ELA lakes (Table 2.4).

Base cations generally increased with warm, dry conditions in these alpine ponds and ELA lakes (Table 2.4). The increase in ELA lakes was likely associated with return of base cations from the sediments as water renewal time increased (Schindler et al. 1996). Increased base cations in these alpine ponds may also be due to increased diffusion from sediment but also due to increased terrestrial inputs, as mineralization rates increase with temperature (Sommaruga-Wögraph et al. 1997). More concentration by evaporation and less dilution by precipitation during the warm-dry years also likely led to increased base cation concentrations in these alpine ponds.

As base cation concentrations increased, sulfate concentrations decreased in these alpine ponds and nearby alpine lakes during the warm-dry year (Table 2.4). This decrease may be due to increased sulfate uptake by algae as primary productivity likely increased with warmer temperatures (DeNicola 1996). Sulfate concentrations likely decreased during the warm-dry year because of increased microbial sulfate reduction. Higher sulfate concentrations in the cold-wet year (1999) than the warm-dry year (1998) may also be due to release of sulfate stored in the sediment during the dry period at the end of 1998

Table 2.4: Overview of physical and chemical responses to the warm-dry year of 1998 in comparison to the cold-wet year of 1999. Given are the response of the four alpine ponds (South Ridge Two, East Ridge One, East Ridge Two and East Ridge Three), two alpine lakes (Pipit (PP) and Snowflake (SF)) and two inflow streams (Pipit inflow stream (PP IF) and Snowflake inflow stream (SF IF)). Solid arrows indicate if the feature was significantly ($P < 0.1$) higher (▲) or lower (▼) in 1998 over 1999 and the clear arrows (Δ∇) indicate either a lower or higher 'trend' in 1998 over 1999. Also given is the general trend in Lake 239 at the Experimental Lakes Area (ELA) during a warm-dry period in the 1970s and 1980s (Schindler 1990; 1996). Increasing arrows indicate significant higher values (▲) or higher 'trend' (Δ) during the warm-dry period.

	SR2	ER1	ER2	ER3	PP	PIP IF	SF	SF IF	ELA
Mean temperature	▲	▲	▲	▲	▲	▲	▲	▲	▲
Ice-free season length	▲	▲	▲	▲	▲	▲	▲	▲	▲
DIN	∇	=	=	=	▼	=	▼	▼	=
TP	=	=	▲	Δ	▼	▼	=	=	▼
DOC	∇	=	=	=	▼	▼	▼	=	∇
Si	=	=	Δ	=	∇	=	=	▲	▼
Cl	=	Δ	=	▲	=	▼	=	=	?
SO4	=	▼	▼	=	▼	=	∇	=	▲
Na	=	=	=	=	∇	=	=	Δ	▲
K	=	=	Δ	▲	=	=	=	▲	▲
Ca	=	=	Δ	=	∇	=	=	▲	▲
Mg	=	=	Δ	▲	▼	=	=	▲	▲
Alk	=	=	▲	▲	=	=	▲	▲	▲
pH	▲	=	▲	▲	▲	▲	▲	▲	▲
Cond	=	=	▲	▲	▼	=	Δ	▲	?

(Eimers and Dillon 2002). In contrast to these results, sulfate concentrations in ELA lakes increased during the warm-dry period (Table 2.4; Schindler et al. 1996).

As base cations increased and sulfate decreased it was not surprising that conductivity, alkalinity and pH increased in these alpine ponds and nearby alpine lakes (Table 2.4). A strong positive pH-temperature relationship has been found in other alpine lakes (Psenner and Schmidt 1992; Sommaruga-Wögraph, et al. 1997; Koinig et al. 1998). This increase in pH has been related to increased terrestrial weathering rates, longer water-retention times, higher biotic biomass production, and stronger reduction processes at the sediment-water interface (Psenner and Schmidt 1992; Sommaruga-Wögraph, et al. 1997; Koinig et al. 1998).

Silica concentrations in these alpine ponds were similar during both years, except for a slight increase in concentrations in ER2 early in the ice-free season during the warm-dry year (Table 2.4). This slight increase may reflect increased weathering in the drainage basin, as suggested by the increased Si concentrations in Snowflake Lake's inflow stream during the warm-dry year. These findings contrast results from ELA, where Si concentrations in lakes decreased during the warm-dry period as terrestrial weathering and stream exports decreased (Table 2.4; Schindler et al. 1996). Even if Si inputs to alpine ponds changed significantly during the warm-dry year, diatom uptake would likely obscure any change in inflow concentrations (as seen in Snowflake Lake (Table 2.4)) and water column Si concentrations would remain unchanged.

DOC concentrations in alpine ponds I studied were similar during both years, whereas DOC concentrations decreased in nearby alpine lakes and in lakes at ELA during the warm-dry years. These decreases coincide with less allochthonous DOC inputs (Table 2.4; Schindler et al. 1996). Unchanged DOC concentrations in alpine ponds may indicate autochthonous DOC inputs increased with the warmer temperatures as allochthonous DOC inputs decreased. If this is true UV penetration should increase with a warmer-drier climate as the aromaticity of DOC decreases (McKnight et al. 2001).

N and P concentrations in these alpine ponds were generally similar during the warm-dry year and the cold-wet year (Table 2.4). The significant increase of TP in ER2 and the weak trends in the other two ponds were caused by peaks in nutrient concentrations occurring in only one of the two years. Two of the three nutrient peaks occurred in the warm-dry year which may reflect an increased chance of sediment nutrient release by wind as ponds become shallower in the warm-dry year but these data are insufficient to confirm this possibility.

The lack of a consistent nutrient response to the change in temperature and precipitation in these alpine ponds does not necessarily indicate the nutrient budgets were unaffected but rather any changes in inputs were offset by *in situ* abiotic and biotic controls. *In situ* controls are thought to be important in these alpine ponds, as explained previously. However few ecosystems are capable of maintaining stable nutrient concentrations as their inputs and outputs change. For instance, N and P concentrations in nearby alpine lakes decreased as nutrient concentrations in their inflow streams decreased (Table 2.4). Furthermore, P concentrations decreased in lakes at ELA as terrestrial inputs decreased and *in situ* biological removal increased (Schindler et al. 1996). Conversely, N concentrations in lakes at ELA increased initially as the result of losses from the catchments after forest fire then leveled off to a steady state (Schindler et al. 1996). Of all the chemical constituents, nutrient concentrations respond the least consistently across these aquatic ecosystems.

Conclusions

Results suggest that alpine ponds are physically demanding aquatic ecosystems that will likely become even more physically demanding as the climate warms. Similar to arctic ponds (Douglas and Smol 1999), alpine ponds can be used as an indicator of how climate change may affect other aquatic systems because they are located in an area predicted to have enhanced warming and their physical features are very responsive to changes in temperature and precipitation. Although the organisms that inhabit these ponds are already adapted to a physically variable environment, it is unknown how much additional variability they can tolerate.

REFERENCES

Alexander, V., Whalen, S.C. and Klingensmith, K.M. 1989. Nitrogen cycling in Arctic lakes and ponds. Hydrobiologia **172**: 165-172.

Anderson, R.S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in Western Canada. Journal of Fisheries Research Board of Canada **28**: 311-321.

Anderson, R.S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. Journal of the Fisheries Research Board of Canada **31**: 855-869.

APHA (American Public Health Association), American Water Works Association and Water Environment Federation (1992) Standard Methods for the Examination of Water and Wastewater. 18th Ed. APHA, Washington, D.C.

Baron, J.A., Rueth, H.M., Wolfe, A.M., Nydick, K.R., Allstott, E.J., Minear, J.T. and Moraska, B. 2000. Ecosystem response to nitrogen deposition in the Colorado Front Range. Ecosystems **3**: 352-368.

Beder, K. 1967. Ecology of the alpine vegetation of Snow Creek Valley, Banff National Park, Alberta. M.Sc. thesis, University of Calgary, Calgary, Alberta, Canada.

Beniston, M., Rebetez, M., Giorgi, F. and Marinucci, M.R. 1994. An analysis of regional climate change in Switzerland. Theoretical and Applied Climatology **49**: 135-159.

Black, J.H. 1976. Environmental fluctuations in central Oklahoma temporary ponds. Proceedings from the Oklahoma Academy of Sciences. **56**: 1-8.

Bowman, W.D., Theodose, T.A., Schardt, J.C. and Conant, R.T. 1993. Constraints of nutrient availability of primary production in two alpine tundra communities. Ecology **74**: 2085-2097.

Campbell, D.H., Baron, J.A., Tonnessen, K.A., Brooks, P.S. and Schuster, P.F. 2000. Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resources Research **36**: 37-47.

Covich, A.P., Fritz, S.C., Lamb, P.J., Marzolf, R.D., Matthews, W.J., Poiani, K.A., Prepas, E.E., Richman, M.B. and Winter, T.C. 1997. Potential effects of climate

change on aquatic ecosystems of the Great Plains of North America. Hydrological Processes **11**: 993-1021.

Daborn, G.R. 1974. Biological features of an Aestival pond in Western Canada. Hydrobiologia **44**: 287-299.

Daborn, G.R. 1976a. Physical and chemical features of a vernal temporary pond in Western Canada. Hydrobiologia **51**: 33-38.

Daborn, G.R. 1976b. The life-cycle of *Eubranchipus bundyi* (Forbes) (Crustacea: Anostraca) in a temporary vernal pond in Alberta. Canadian Journal of Zoology **54**: 193-201.

Daborn, G.R. and Clifford, H.F. 1974. Physical and chemical features of an aestival pond in Western Canada. Hydrobiologia **44**: 43-59.

Danks, H.V. 2000. Insect cold hardiness: A Canadian perspective. CryoLetters **21**: 297-308.

DeNicola, D.M. 1996. Periphyton responses to temperature at different ecological levels. *In* An introduction to algal ecology in freshwater benthic habitats. *Edited by* R.J. Stevenson, M.L. Bothwell and R.L. Lowe. Academic Press, Toronto. pp. 150-183.

Douglas, M.S.V. 1989. Taxonomic and ecological characterization of freshwater diatoms from the sediments of 36 high Arctic ponds (Cape Herschel, Ellesmere Island, N.W.T., Canada). M.Sc. thesis Queen's University, Kingston, Ontario, Canada.

Douglas, M.S.V. and Smol, J.P. 1994. Limnology of high arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.). Archiv für Hydrobiologie **131**: 401-434.

Douglas, M.S.V. and Smol, J.P. 1999. Freshwater diatoms as indicators of environmental changes in the high Arctic. *In* The Diatoms: Applications for the Environmental and Earth Sciences. *Edited by* E.F. Stoermer and J.P. Smol. Cambridge University Press, Cambridge. pp. 227-44.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. and Mearns, L. 2000. Climate extremes: Observations, modeling and impacts. Science **289**: 2068-2074.

Eimers, M.C. and Dillon, P.J. 2002. Climate effects on sulphate flux from forested catchments in south-central Ontario. Biogeochemistry **61**: 337-355.

Environment Canada. 2002. Database for Banff Town Site available through Environment Canada's Meteorological Service of Canada. http://www.msc-smc.ec.gc.ca/climate/station_catalogue/index_e.cfm

Environmental Protection Agency. 1993. Method 300.0. Determination of Inorganic Anions by Ion Chromatography. Revision 2.1. John D. Pfaff. United States Environmental Protection Agency Environmental Monitoring Systems Laboratory, Cincinnati, OH 45268. Office of Research and Development.

Fyfe, J.C. and Flato, G.M. 1999. Enhanced climate change and its detection over the Rocky Mountains. Journal of Climate **12**: 230-243.

Giorgi, F., Hurrell, J.W. and Marinucci, M.R. 1997. Elevation dependency of the surface climate change signal: A model study. Journal of Climate **10**: 288-296.

Hartland-Rowe, R. 1972. The limnology of temporary waters and the ecology of Euphyllopoda. *In* Essay in Hydrobiology. *Edited by* P.B. Clarke and R. Wootton. University of Exeter, Devon, England. pp. 15-31.

Havens, K.E. 1994. Experimental perturbation of a freshwater plankton community: A test of hypotheses regarding the effects of stress. Oikos **69:** 147-153.

Hebert, P.D. and Hann, B.J. 1989. Patterns in the composition of Arctic tundra pond microcrustacean communities. Canadian Journal of Fisheries and Aquatic Sciences **43**: 1416-1425.

Hobbie, J.E. 1973. Arctic Limnology: A review. *In* Alaskan Arctic Tundra *Edited by* M.E. Britton. Arctic Institute of North America Technical Paper 25. pp.127-168.

Hobbie, J.E. 1980. Limnology of Tundra Ponds: Barrow Alaska. Dowden, Hutchinson and Ross, Inc., Pennsylvania, United States.

Hogg, I.D., Williams, D.D., Eadie, J.M. and Butt, S.A. 1995. The consequences of global warming for stream invertebrates: a field simulation. Journal of Thermal Biology. **20**: 199-206.

Holland, W. D. and Coen, G. M. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume II: Soil and Vegetation Resources and Map Supplement. 1982. Alberta Institute of Pedology.

Intergovernmental Panel of Climate Change. 2001. Climate Change 2001: The Scientific Basis http://www.grida.no/climate/ipcc_tar/wg1/index.htm

Wellborn, G.A., Skelly, D.K. and Werner, E.E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics **27**: 337-363.

Koinig, K.A., Schmidt, R., Sommaruga-Wögraph, S., Tessadri, R. and Psenner, R. 1998. Climate change as the primary cause for pH shifts in a high alpine lake. Water, Air and Soil Pollution **104**: 167-180.

Lafrançois, B.M. 2002. Algal and invertebrate response to atmospheric nitrogen deposition in Rocky Mountain lakes. Ph.D. thesis, Colorado State University, Fort Collins, Colorado, United States.

Lahr, J. 1997. Ecotoxicology of organisms adapted to life in temporary freshwater ponds in arid and semi-arid regions. Archive of Environmental Contamination and Toxicology **32**: 50-57.

Lamontagne, S., Donald, D.B. and Schindler, D.W. 1994. The distribution of four *Chaoborus* species (Diptera: Chaoboridae) along an elevation gradient in Canadian Rocky Mountain lakes. Canadian Journal of Zoology. **72**: 1531-1537.

Luckman, B.H. and Kavanagh, T. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. Ambio **29**: 371-380.

Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T., Assel, R.A., Barry, R.G., Card, V., Kuususto, E., Granin, N.G., Prowse, T.D., Stewart, K.M. and Vuglinshki, V.S. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science **289**: 1743-1746.

Mann, M.E., Bradley, R.S. and Hughes, M.K. 1999. Northern Hemisphere temperatures during the past millennium: Inferences, uncertainties and limitations. Geophysical Research Letters **26**: 759-762.

McKnight, D.M., Boyer, E.W., Doran, P., Westerhoff, P.K., Kulbe, T. and Andersen, D.T. 2001. Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. Limnology and Oceanography **46**: 38-48

Meehl, G.A., Zwiers, F., Evans, J., Knutson, T., Mearns, L. and Whetton, P. 2000. Trends in extreme weather and climate events: Issues related to modeling extremes in projections of future climate change. Bulletin of the American Meteorological Society **81**: 427-436.

Miller, M.C., Prentki, R.T. and Barsdate, R.J. 1980. Physics. *In* Limnology of Tundra Pond. *Edited by* J.E. Hobbie. Dowden, Hutchinson and Ross, Inc., Pennsylvania, United States. pp. 51-75.

Moore, M.V., Folt, C.L. and Stemberger, R.S. 1996. Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. Archiv für Hydrobiologie **135**: 289-319.

Morris, D.P. and Lewis, W.M. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biology **20**: 315-327.

Murphy, J. and J.P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytical Chemistry Acta **27**: 31-36

Neldner, K.N. and Pennak, R.W. 1955. Seasonal faunal variations in a Colorado alpine pond. American Midland Naturalist **53**: 419-430.

Parmesan, C., Root, T.L. and Willig, M.R. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society **81**: 443-450.

Paul, A.J., Leavitt, P.R., Schindler, D.W. and Hardie, A.K. 1995. Direct and indirect effects of predation by a calanoid copepod (subgenus: *Hesperodiaptomus*) and of nutrients in a fishless alpine lake. Canadian Journal of Fisheries and Aquatic Sciences **52**: 2628-2638.

Pichler, W. 1939. Der Almtümpel als Lebensstätte. Eine ökologische Studie. Bioklimatische Beibl. **6**: 85-89.

Prentki, R.T., Miller, M.C., Barsdate, R.J., Alexander, V., Kelley, J. and Coyne, P. 1980. Chemistry. *In* Limnology of Tundra Pond. *Edited by* J.E. Hobbie. Dowden, Hutchinson and Ross, Inc., Pennsylvania, United States. pp. 76-178.

Prepas, E.E. and Rigler, F.H. 1982. Improvements in quantifying the phosphorus concentration in lake water. Canadian Journal of Fisheries and Aquatic Sciences **39**: 822-829.

Psenner, R. and Schmidt, R. 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. Nature **356**: 781-783.

Robertson, D.M. 1989. The use of water temperature and ice cover as climatic indicators. Ph.D. thesis University of Wisconsin, Madison, Wisconsin, United States.

SAS Institute Inc. 1996. JMP IN version 3.2.1.

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. Hydrological Processes **11**: 1043-1067.

Schindler, D.W. 2000. Aquatic problems caused by human activities in Banff National Park, Alberta, Canada. Ambio **29**: 401-407.

Schindler, D.W., Bayley, S.E. and Parker, B.R. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, Northwestern Ontario. Limnology and Oceanography **41**: 1004-1017.

Schindler, D.W., Beaty, E.J., Fee, E.J., Cruikshank, D.R., DeBruyn, E.R., Findley, D.L., Linsey, G.A., Shearer, J.A., Stainton, M.P. and Turner, M.A. 1990. Effects of climate warming on lakes of the Central Boreal Forest. Science **250**: 967-970.

Scheffer. M. 1998. Ecology of Shallow Lakes. Chapman and Hall, London.

Schmitz, E.H. 1959. Seasonal biotic events in two Colorado alpine tundra ponds. The American Midland Naturalist **61**: 424-445.

Scully, N. M. and Lean, D. R. S. 1994. The attenuation of ultraviolet radiation in temperate lakes. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie **43**:134-144.

Sickman, J.O. 2001. Comparative analysis of nitrogen biogeochemistry in high elevation ecosystems. Ph.D. thesis, University of California, Santa Barbara, California, United States.

Sommaruga-Wögraph, S., Koinig, K.A., Schmidt, R., Sommaruga, R., Tessadri, R. and Psenner, R. 1997. Temperature effects on the acidity of remote alpine lakes. Nature **387**: 64-67.

Stainton, M.P., Capel, M.J. and Armstrong, F.A.J. 1977. The Chemical Analysis of Freshwater. 2nd Ed. Fisheries Environment Canada Miscellaneous Special Publication. 25: 180 pp.

Tank, S.E. 2002. Effects of Ultraviolet Radiation on Benthic Assemblages of Montane Lakes. M.Sc. thesis. University of Alberta, Edmonton, Canada.

Vinebrooke, R.D. and Leavitt, P.R. 1999. Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. Journal of North American Benthological Society **18**: 14-32.

Webb, B.W. 1996. Trends in stream and river temperature. Hydrological Processes **10**: 205-226.

Williams, D.D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of North American Benthological Society **15**: 634-650.

Zar, J.H. 1999. Biostatistical Analysis. Prentice Hall, New Jersey.

Zhang, X., Vincent, L.A., Hogg, W.D. and Niitsoo, A. 2000. Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean **38**: 395-429.

CHAPTER 3: PLANKTONIC AND EPIPELIC ALGAL COMMUNITIES AND THEIR RELATIONSHIP TO PHYSICAL AND CHEMICAL VARIABLES IN ALPINE PONDS IN BANFF NATIONAL PARK, CANADA

INTRODUCTION

Mountain ecosystems may be particularly sensitive to environmental change (Hauer et al. 1997; Bowman 2000). Alpine aquatic ecosystems, for example, are particularly sensitive to increases in atmospheric nitrogen (N) deposition because their steep, sparsely vegetated watersheds retain little nitrogen (Williams et al. 1996; Baron et al. 2000). Increased nitrogen loading is linked to eutrophication in some sub-alpine and alpine lakes in the western United States (Baron et al. 2000; Wolfe et al. 2001). Furthermore, alpine ecosystems may be sensitive to global climate change because snow-albedo feedback in high elevation sites is predicted to decrease, causing faster warming than at low elevation sites (Giorgi et al. 1997; Fyfe and Flato 1999). Climate-sensitive variables, such as conductivity, dissolved organic carbon and the elevation of tree-line, have been identified as predictors of algal communities in mountain lakes and ponds (Vinebrooke and Leavitt 1999). Although we are beginning to understand the impacts of environmental change on high elevation lakes, little is known regarding how alpine ponds will respond.

Alpine ponds are numerous, with over 3000 located in Banff National Park (6,641 km^2), Canada. Despite their abundance, only five studies have been published since North American alpine ponds were described and classified by Ives in 1941. In the Colorado Rocky Mountains, very basic seasonal limnological changes were described in one large (Neldner and Pennak 1955) and two small alpine ponds (Schmitz 1959). In the Canadian Rocky Mountains, planktonic crustaceans were surveyed in 14 alpine ponds (Anderson 1971; Anderson 1974) and planktonic and benthic algal communities were surveyed in two alpine ponds (Vinebrooke and Leavitt 1999). A comprehensive description of the physical and chemical features and algal communities that characterize several alpine ponds has yet to be completed. However, a recent study of five alpine ponds in Banff National Park found that length of the ice-free season, water temperature, maximum depth, pH and conductivity respond to changes in temperature and precipitation (Chapter 2).

Multivariate gradient techniques such as redundancy analysis have been applied to survey data to clarify relationships between environmental variables and algal communities (Vinebrooke and Leavitt 1999; Lafrançois 2002). These methods allow prediction of the impact of future environmental change on algal communities (Vinebrooke and Leavitt 1999; Lafrançois 2002) or deduction of past environmental conditions based on current algal-environmental relationships (Smol and Cumming 2000). However, most studies base their predictions and deductions on surveys from one year even though environmental conditions (Chapter 2; Bennion and Smith 2000) and the controls on the algal communities vary over time (Chapter 4; Rosemond et al. 2000; Villar-Argaiz et al. 2001). Consequently, predictions and deductions may change depending on which year was sampled.

The aim of this study was to better understand the limnology of alpine ponds and predict how their algal communities may respond to environmental change. The main objectives were to identify the physical and chemical variables that best explain phytoplankton and epipelon abundance and community composition in alpine ponds and to determine if the physical and chemical variables that best explain these patterns differ between two summers with different temperature and precipitation. In the process, I 1) describe the physical and chemical limnology across 28 alpine ponds; 2) assess nutrient limitation with nitrogen to phosphorus ratios; and 3) describe the phytoplankton and epipelon communities across 28 alpine ponds in Banff National Park. To address these objectives I surveyed 14 ponds in 1999 and 28 ponds in 2000. I recorded 15 physical and chemical variables and sampled planktonic and epipelic (sediment-living) algal communities at each pond then analyzed the data using multivariate gradient techniques. Phytoplankton and epipelon abundance and community composition were inferred from pigment concentrations derived from high performance liquid chromatography (HPLC).

METHODS

Study site

The survey ponds are located in the alpine ecoregion (2150 - 2570 m above sea level; 51° 27' - 51° 44'N, 115° 39' - 115° 56'W) in the eastern front ranges of the Rocky Mountains in Banff National Park, Alberta, Canada (Figure 3.1). Alpine ponds in this area typically have drainage basins consisting of a mosaic of small patches of exposed sedimentary rock, including limestone, shale and sandstone and sparsely vegetated pockets on orthic eutric brunisol soils (Holland and Coen 1982). Vegetation on sites with soils include white heather (*Cassiope tetragona*), yellow heather (*Phyllodoce glanduliflora*), arctic willow (*Salix arctica*), white mountain avens (*Dryas hookeriana*), bladder locoweed (*Oxytropis podocarpa*), sedges (*Carex* spp.), lichens, kruppelholz Engelmann spruce (*Picea engelmannii*) and kruppelholz alpine fir (*Abies lasiocarpa*) (Beder 1967).

Long-term climate records are not available for high elevation sites in the Canadian Rockies. The nearest long-term climate record is for the Banff town site (1383 m above sea level; 51°11'N, 115° 34'W), 29-64 km south and 813-1173 m lower than the survey ponds (Figure 3.1; Environment Canada 2002). Mean annual air temperature for the last 100 years at Banff Town site was 2.5°C. Mean summer (June - September) air temperature was 12.1°C but daily temperatures ranged from below 0 °C to above 27 °C. Of the last 100 years, the summer of 1999 was the 11th coolest (mean = 11.0°C) and the summer of 2000 was the 16th coolest (mean = 11.4°C) (Appendix 1). Mean annual precipitation for the last 100 years at Banff town site was 467 mm, with 267 mm as rain and 200 mm as snow. Of the last 100 years, the year leading up to and including the ice-free season of 1999 (October 1998 - September 1999) was the 37th wettest (495 mm) and the year leading up to and including the ice-free season of 2000 (October 1999 - September 2000) was the 10th driest (362 mm). Therefore, in the vicinity of the study ponds the summer of 1999 was slightly cooler and much wetter than the summer 2000.

Sampling protocol and analyses

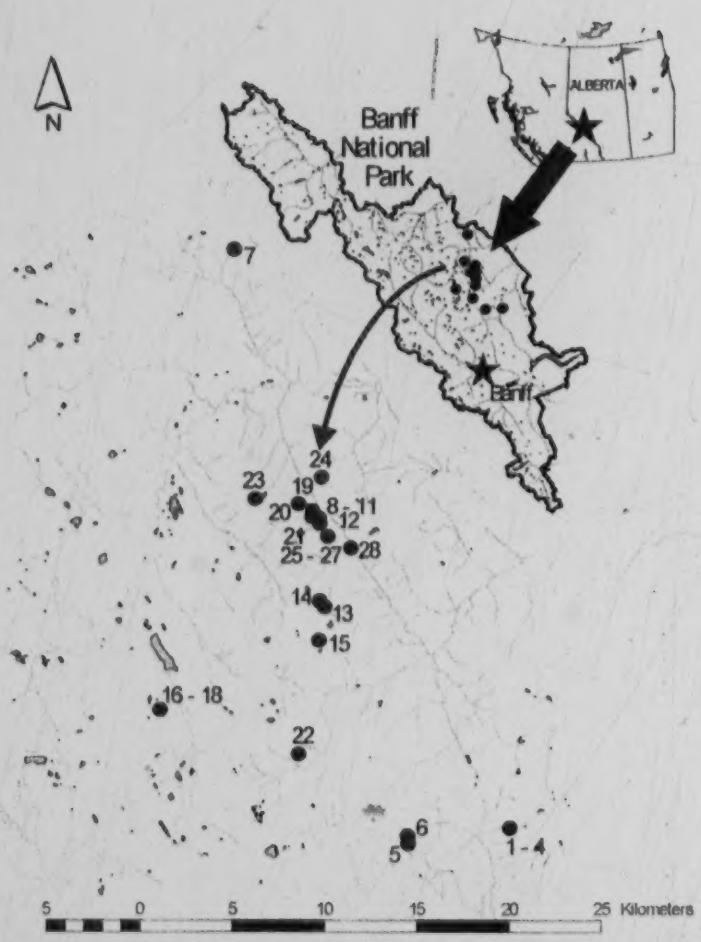
I sampled 14 ponds once during the period of July 23-27, 1999. These 14 ponds and an additional 14 ponds were sampled once during the period of July 25-30, 2000 (Figure

3.1). Ponds were selected to cover a range of elevations, drainage basin characteristics, sizes, depths and bottom types.

Latitude (LAT), longitude (LONG) and elevation (ELV) were determined with a Global Position System and 1:50000 maps. Approximate surface area (AREA) of each pond was determined by visual estimation. Approximate maximum water depth (DEPTH) of each pond was determined with a depth line. I categorized the bottom (BOTT) as sediment (BTS), sediment and rock (BTSR), or rock (BTR) and the drainage basin (DRBN) as meadow (DBM), meadow and rock (DBMR), or rock (DBR). Water temperature (WTEMP) was measured with a handheld thermometer 0.2 m below the surface at the time of sampling. Conductivity (COND) was measured *in situ* with a Cole-Parmer® handheld TDSTestr 40 with automatic temperature correction.

Water was sampled by plunging pre-rinsed 500 ml polyethylene bottles below the water surface 0.5 m from the ponds' edge. Half of the water was filtered in the field through Whatman® GF/F filters. Samples were analyzed for ammonium (NH_4-N), nitrite plus nitrate (NO_2-N+NO_3-N), total phosphorus (TP), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), silica (Si), alkalinity (ALK) and pH by the University of Alberta's Water Laboratory (Chapter 2).

Algal nutrient limitation was assessed with DIN:TP ratios from the water column. DIN:TP, rather than TN:TP or DIN:SRP, agrees most strongly with nutrient limitation bioassays in other mountain lakes and ponds (Morris and Lewis 1988; Sickman 2001). Ratios less than 1 indicate N-limitation and greater than 4 indicate P-limitation. Ratios between 1 and 4 indicate intermediate limitation, i.e., reciprocal or co-limitation by N and P (Morris and Lewis 1988; Sickman 2001).



Number	Pond Name	Abbreviation
1	Bighorn East	BE
2	Bighorn Middle Large	BML
3	Bighorn Middle Small	BMS
4	Bighorn West	BW
5	Cuthead Large	CL
6	Cuthead Small	CS
7	Divide Pond	DP
8	East Ridge One	ER1
9	East Ridge Two	ER2
10	East Ridge Three	ER3
11	East Ridge Four	ER4
12	Grouse Pond	GP
13	Harrison North East	HNE
14	Harrison North West	HNW
15	Harrison South	HS
16	Mount Douglas Large	MDL
17	Mount Douglas Small One	MDS1
18	Mount Douglas Small Two	MDS2
19	North Pond One	NP1
20	North Pond Two	NP2
21	North Pond Three	NP3
22	Panther Pond Two	PP2
23	Pipit Pond	PIP
24	Saddle Pond Center	SPC
25	South Gully Three	SG3
26	Snowflake Pond	SFP
27	South Ridge Two	SR2
28	Toad Pond	TP

Figure 3.1: Study ponds are located on north of Banff Town Site (51° 27' - 51° 44'N, 115° 39' - 115° 56'W) in Banff National Park, Alberta, Canada. Ponds are numbered alphabetically and the full name and abbreviations are given.

Phytoplankton were sampled by filtering 0.4 - 1 L of pond water through Whatman GF/F filters and epipelon were sampled by pooling three sediment surface samples collected with plastic Petri dishes (4.7 cm diameter × 0.5 cm depth) (Vinebrooke and Leavitt 1999). Filters and Petri dishes were wrapped in aluminium foil and stored in the dark at -20 °C until further analysis. Samples were freeze-dried for 24 h then extracted in a 10 ml mixture of acetone, methanol and water (80:15:5 by volume) for 24 h at 10 °C in the dark. Extracts were filtered (0.22 μm Acropore Nylon membrane), dried under nitrogen gas and stored in the dark at –30 °C under nitrogen gas until analysis. Dried extracts were dissolved in a known volume of injection solvent of acetone, ion pairing reagent and methanol (70:25:5 by volume) containing 3.2 mg L^{-1} of the internal standard Sudan II. Pigments were separated by high performance liquid chromatography (HPLC) with a Hewlett Packard® Model 1100 and a Rainin Model 200 C18 column (Vinebrooke et al. 2002).

Algal abundance and composition were inferred from concentrations of taxonomically diagnostic chlorophylls and carotenoids derived from high performance liquid chromatography (HPLC) (Jeffrey et al. 1997). Major algal groups identified with HPLC included cryptophytes (alloxanthin (All)), chlorophytes (chlorophyll *b* (Chlb), lutein (Lut), violaxanthin (Viol)), chromophytes (diadinoxanthin (Diad), fucoxanthin (Fuc), chlorophyll *c* (Chlc)), including diatoms (diatoxanthin (Diat)) and Cyanobacteria (echinenone (Ech), canthaxanthin (Can), zeaxanthin (Zea)), including colonial forms (myxoxanthophyll (Myx)).

Statistical Analysis

Physical and chemical variables were either $\log_{10}$ or square root transformed and chlorophyll *a* concentrations were $\log_{10}$ transformed to approximate normal distribution before statistical analysis (Zar 1999). Two-tailed *t*-tests were used to assess significant differences in the physical and chemical variables between 1999 and 2000. Univariate linear regressions followed by a stepwise backward multiple regression were used to determine significant relationships between DIN:TP ratios and physical and chemical variables in the 28 ponds sampled in 2000 using STATISTICA (StatSoft 1998).

To address the main objectives, the data were grouped into three sets: all 28 ponds sampled in 2000; the 14 ponds sampled in 1999 and the same 14 ponds resampled in 2000. The first dataset was used to identify the best physical and chemical predictors of patterns in phytoplankton and epipelon abundance and community composition across alpine ponds. Comparison of the remaining two datasets test whether these best predictors differed between the two summers. First, Pearson product-moment correlations with Bonferroni-adjusted probabilities were used to detect significant ($P \leq 0.05$) correlations among physical and chemical variables in each of the three datasets using STATISTICA (StatSoft 1998). Second, univariate linear regressions followed by a stepwise backward multiple regression were used to identify the physical and chemical variables that best predict phytoplankton and epipelon abundance (chlorophyll *a*) in each of the three datasets. Finally, physical and chemical variables that best predict patterns in the phytoplankton and epipelon community composition in each of the three datasets were identified with ordination analysis (CANOCO (canonical community ordination) version 4; ter Braak and Šmilauer 1998).

Detrended correspondence analysis (DCA) established that pigment variation was best explained by the linear response model, redundancy analysis (RDA) (ter Braak and Šmilauer 1998). Pigment concentrations were $\log_{10}(x+1)$ transformed to reduce the influence of rare or dominant pigments, which might otherwise dominate the analysis and to increase normality of the data (ter Braak and Šmilauer 1998). Si was excluded from the RDA because it was not measured in all ponds. Nominal variables (BOTT and DRBN) were included as binary codes (value 0 or 1). Environmental datasets were screened to eliminate physical and chemical covariables and insignificant variables with a correlation matrix, forward selection and a series of partially constrained RDAs (Vinebrooke and Graham 1997). The final RDA models for each dataset and algal community included just independent and significant ($\alpha < 0.1$) variables. The significance of the first two ordination axes was tested against 1000 Monte Carlo permutations (ter Braak and Šmilauer 1998). Variation partitioning was used to estimate how much of the variation in pigment concentrations can be explained by each physical and chemical variable in the final RDA (Anderson and Gribble 1998).

In RDA triplots, ponds are represented as points and pigments and quantitative environmental variables are represented as arrows. The length of an arrow corresponds to the relative importance of that environmental variable in explaining the observed variance in the pigment data. The length of a pigment arrow corresponds to its relative importance in the differences across ponds. The placement of arrows relative to other arrows represents their approximate correlation to each other – arrows placed close together are positively correlated; arrows at right angles are not correlated; and arrows pointing in opposite directions are negatively correlated. The distance between points representing ponds is meaningless but the relationship between ponds and pigment and environmental arrows can be obtained by projecting a line from the pond perpendicular to the arrows. The further along the arrow in the positive direction this projected lines falls, the more positively correlated the pond is to the pigment and environmental variables.

RESULTS

Physical and chemical features

Elevation of the 28 ponds ranged from 2150 to 2570 m asl (Table 3.1; Appendix 3). Most ponds (68%) were located in alpine meadows and only three ponds were located in rock basins. Ponds were small, with surface areas ranging from 50 to 6000 m^2 and shallow, with depths ranging from 10 to 200 cm (Table 3.1). Most ponds (86%) were less than 2000 m^2 in area and 90 cm deep. Ponds with large surface areas tended to be deep. Ponds ranged in shape from rectangular to circular and most had steep-sided, U-shaped basins. Most ponds were found in inter-connected groups of 2 to 4 and the remaining ponds lacked inflows and outflows. Most ponds (62%) had bottoms consisting of dark, highly organic unconsolidated sediment and only one (HS) had a bottom consisting of rock and no sediment. Higher elevation ponds were more likely to have bottoms and drainage basins containing rock whereas lower elevation ponds were more likely to have bottoms consisting of sediment and drainage basins consisting of alpine meadows. Water temperatures ranged from 0 to 24 °C across the 28 ponds in 2000 (Table 3.1). In the 14 ponds sampled in both years, surface areas were smaller ($P < 0.1$) in 2000 then in 1999 (Table 3.1).

Table 3.1: Mean (standard deviation), minimum and maximum values for physical, chemical, biological variables measured in 28 alpine ponds in 2000 Banff National Park, Canada. Means (standard deviation) are also given for 14 ponds sampled in both 1999 and 2000. Significant differences between 1999 and 2000 data are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.01$).

	2000 (n = 28)			1999 (n = 14)	2000 (n = 14)
Variable	Mean (SD)	Min.	Max.	Mean (SD)	Mean (SD)
Elevation (m)	2299 (95)	2150	2570	2282 (34)	2282 (34)
Surface area (m^2)	1377 (1397)	50	6000	*853 (1041)	682 (957)
Maximum depth (cm)	50 (41)	10	200	53 (25)	38 (23)
Water temperature (°C)	11 (6)	0	24	14 (3)	15 (6)
Dissolved organic carbon (mg L^{-1})	5.4 (5.5)	0.20	17.93	7.7 (3.7)	8.6 (5.7)
Conductivity (µS cm^{-1})	74.5 (50.3)	11.1	190.0	60.3 (46.5)	77.0 (62.4)
Alkalinity (meq L^{-1})	1.24 (0.99)	0.14	4.46	0.61 (0.47)	0.75 (0.56)
pH	7.7 (0.6)	6.4	8.4	*6.9 (0.7)	7.3 (0.7)
Ammonium (µg L^{-1})	24.2 (23.5)	<1.0	100.2	***9.6 (7.7)	34.4 (25.7)
Nitrite+Nitrate (µg L^{-1})	22.1 (31.7)	1.9	111.9	4.4 (2.9)	3.9 (1.5)
Dissolved inorganic nitrogen (µg L^{-1})	46.3 (29.7)	5.2	116.9	***14.0 (8.8)	38.3 (25.6)
Total phosphorus (µg L^{-1})	51.3 (62.2)	2.9	272.3	*30.7 (29.4)	68.4 (66.9)
Soluble reactive phosphorus (µg L^{-1})	3.4 (2.0)	<1.0	9.2	3.8 (2.2)	4.1 (1.7)
DIN:TP	3.6 (5.9)	0.02	22.65	0.7 (0.7)	0.8 (0.5)
Silica (mg L^{-1})	0.86 (0.76)	0.05	2.42	1.18 (0.92)	0.86 (0.81)
Phytoplankton abundance (µg L^{-1})	2.34 (5.31)	0.10	27.86	1.23 (1.59)	4.07 (7.20)
Epipelon abundance (µg cm^{-2})	9.78 (9.68)	0.67	39.31	**1.45 (1.37)	6.66 (7.12)

DOC concentrations were fairly high in comparison to alpine lakes and streams (Table 3.1). Ponds with the lowest DOC concentrations were typically found at higher elevations and had rocky bottoms, rocky drainage basins and large surface areas. Ponds were relatively dilute (conductivity < 190 μS cm^{-1}) suggesting that seepage rather than evaporation was a predominant water output. Low conductivity also suggests that precipitation rather than seepage was an important water input. Alkalinity was fairly low and most ponds had close to neutral pH. This is not surprising given the limestone bedrock in the ponds' drainage basins. Nitrogen and phosphorus were typically above detection (1 μg L^{-1}; Table 3.1). Ponds with higher nitrogen concentrations typically had lower phosphorus concentrations, larger surface areas and rocky bottoms and were found at higher elevations. Silica was below 2.4 mg L^{-1} but always above detection (Table 3.1). In the 14 ponds sampled in both 1999 and 2000, pH, NH_4-N, DIN and TP were higher ($P < 0.1$) in 2000 than 1999 (Table 3.1).

Correlation analysis of the physical and chemical variables measured in the 28 ponds in 2000 showed that TP and DIN:TP ratios and alkalinity and pH were significantly correlated (Table 3.2). Correlation analysis of the physical and chemical variables measured in the 14 ponds in 1999 and 2000 showed that alkalinity and conductivity were significantly correlated (Table 3.3 and 3.4).

Nutrient limitation

Based on DIN:TP ratios, 6 ponds were P-limited, 11 ponds were N-limited, 5 ponds had intermediate limitation and 6 ponds were N-limited one year and had intermediate limitation the other (Figure 3.2). Ponds with high DIN:TP ratios tended to have deep water (Figure 3.2), large surface areas (>2000 m^2), rocky bottoms and rocky drainage basins and were found at higher elevations (>2300 m). Multiple regression analysis identified elevation and water temperature as the strongest predictors of DIN:TP ratios in the 28 ponds sampled in 2000 ($\log_{10}$DIN:TP = -7.31 + 0.0036ELV – 0.29WTEMP; $P < 0.001$; $r^2 = 0.56$; $P_{elv} < 0.001$; $P_{wtemp} = 0.003$). Elevation and water temperature were both highly related to TP (Table 3.2).

Table 3.2: Pearson correlation matrix for all physical and chemical variables measured in 28 alpine ponds in Banff National Park during late July 2000. Bonferroni adjusted correlations at $P < 0.05$ are noted (*). See methods for abbreviations.

	ELV	AREA	DEPTH	BOTT	DRBN	WTEMP	NH_3-N	NO_2-N+ NO_3-N	TP	SRP	DIN:TP	DOC	Si	ALK	pH	COND
ELV	1.00															
AREA	0.27	1.00														
DEPTH	0.44	0.78	1.00													
BOTT	0.66	0.17	0.31	1.00												
DRBN	0.50	0.50	0.56	0.51	1.00											
WTEMP	-0.30	-0.46	-0.47	-0.43	-0.52	1.00										
NH_3-N	0.03	-0.40	-0.27	0.14	-0.27	0.44	1.00									
NO_2-N+NO_3-N	0.41	0.59	0.53	0.34	0.59	-0.58	-0.58	1.00								
TP	-0.68	-0.47	-0.54	-0.45	-0.55	0.65	0.22	-0.57	1.00							
SRP	-0.29	-0.28	-0.31	-0.22	-0.55	0.44	0.30	-0.36	0.60	1.00						
DIN:TP	0.64	0.45	0.53	0.52	0.56	-0.60	-0.07	0.73	***-0.87**	-0.45	1.00					
DOC	-0.37	-0.70	-0.59	-0.41	-0.60	0.73	0.50	-0.76	0.60	0.40	-0.63	1.00				
Si	-0.24	-0.35	-0.33	-0.27	-0.18	-0.14	-0.23	-0.04	-0.02	-0.05	-0.02	-0.07	1.00			
ALK	-0.17	0.18	-0.09	-0.10	0.29	-0.40	-0.28	0.15	-0.10	-0.30	0.07	-0.45	0.53	1.00		
pH	0.16	0.39	0.16	0.31	0.43	-0.58	-0.34	0.36	-0.39	-0.35	0.36	-0.68	0.44	***0.83**	1.00	
COND	0.17	0.28	0.18	0.22	0.04	-0.10	0.19	-0.06	-0.23	0.11	0.19	-0.35	0.17	0.25	0.45	1.00

Table 3.3: Pearson correlation matrix for all physical and chemical variables measured in 14 alpine ponds in Banff National Park during late July 1999. Bonferroni adjusted correlations at $P < 0.05$ are noted (*). See methods for abbreviations.

	ELV	AREA	DEPTH	BOTT	WTEMP	NH_3-N	NO_2-N+ NO_3-N	TP	SRP	DIN:TP	DOC	ALK	pH	COND
ELV	1.00													
AREA	-0.36	1.00												
DEPTH	-0.01	0.73	1.00											
BOTT	0.56	-0.05	-0.07	1.00										
WTEMP	-0.34	-0.43	-0.56	-0.33	1.00									
NH_3-N	-0.27	0.35	0.00	0.42	0.02	1.00								
NO_2-N+NO_3-N	0.22	0.22	0.30	0.21	-0.13	0.21	1.00							
TP	-0.14	0.39	0.07	-0.21	0.19	-0.02	-0.30	1.00						
SRP	0.28	-0.21	0.24	0.09	-0.13	-0.08	0.46	-0.27	1.00					
DIN:TP	0.04	0.18	0.17	0.51	-0.23	0.72	0.66	-0.54	0.37	1.00				
DOC	0.34	-0.57	-0.49	-0.24	0.51	-0.64	-0.27	0.30	-0.20	-0.72	1.00			
ALK	0.03	0.39	0.30	0.33	-0.51	0.53	0.66	-0.53	0.12	0.85	-0.71	1.00		
pH	-0.07	0.51	0.35	0.45	-0.36	0.69	0.61	-0.36	0.10	0.89	-0.75	0.90	1.00	
COND	0.02	0.37	0.31	0.25	-0.52	0.47	0.67	-0.55	0.16	0.81	-0.69	***0.99**	0.86	1.00

Table 3.4: Pearson correlation matrix for all physical and chemical variables measured in 14 alpine ponds in Banff National Park during late July 2000. Bonferroni adjusted correlations at $P < 0.05$ are noted (*). See methods for abbreviations.

	ELV	AREA	DEPTH	BOTT	WTEMP	NH_3-N	NO_2-N+ NO_3-N	TP	SRP	DIN:TP	DOC	ALK	pH	COND
ELV	1.00													
AREA	-0.50	1.00												
DEPTH	-0.26	0.74	1.00											
BOTT	0.56	-0.22	-0.31	1.00										
WTEMP	-0.11	-0.23	-0.33	-0.51	1.00									
NH_3-N	0.61	-0.33	-0.32	0.35	0.28	1.00								
NO_2-N+NO_3-N	-0.07	-0.22	-0.32	0.07	0.26	-0.06	1.00							
TP	-0.10	0.26	-0.02	-0.28	0.49	0.09	0.21	1.00						
SRP	-0.07	0.09	-0.05	-0.13	0.29	0.19	0.16	0.81	1.00					
DIN:TP	0.53	-0.35	-0.16	0.35	-0.14	0.71	-0.32	-0.55	-0.43	1.00				
DOC	0.34	-0.41	-0.37	-0.27	0.50	0.06	-0.01	0.00	-0.28	0.06	1.00			
ALK	-0.22	0.25	-0.01	0.21	-0.16	0.21	-0.27	-0.06	0.20	0.25	-0.62	1.00		
pH	-0.04	0.21	-0.05	0.53	-0.41	0.21	-0.27	-0.24	0.09	0.29	-0.60	0.85	1.00	
COND	-0.42	0.41	0.17	0.06	-0.10	0.16	-0.08	0.02	0.28	0.12	-0.75	***0.91**	0.77	1.00

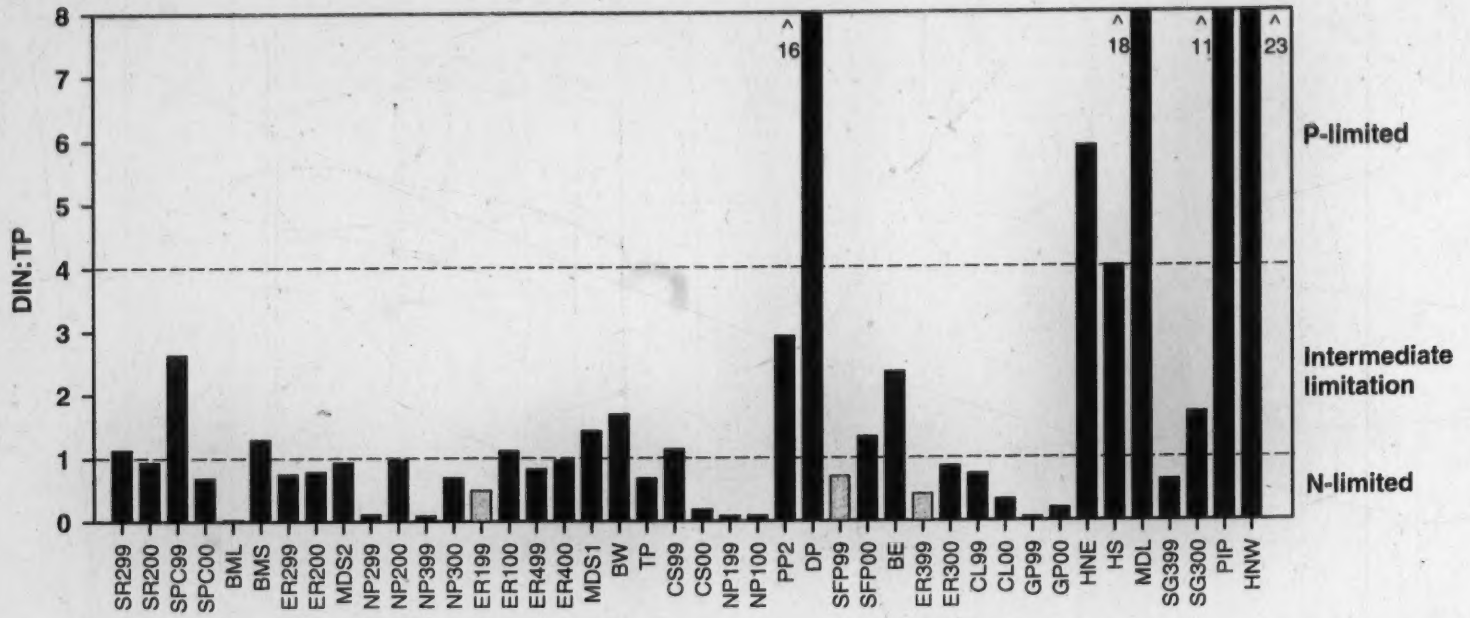


Figure 3.2: DIN:TP ratios measured from the water column of 28 alpine ponds in Banff National Park at end of July 1999 and/or 2000. Ponds are ordered in increasing depth to the right. Ponds sampled in both 1999 and 2000 are grouped together. Dashed lines define nutrient limitation cut-offs as N-limited, DIN:TP ratios ≤ 1 and P-limited, DIN:TP ratios ≥ 4 (Morris and Lewis 1988; Sickman 2001). Ponds with ratios between one and four were considered to have intermediate limitation, i.e., reciprocal or co-limitation by N and P. Grey bars signify ponds that were N-limited in epilithon nutrient enrichment experiments (Chapter 4).

Phytoplankton abundance – environmental relationships

In the 28 ponds sampled in 2000, phytoplankton abundance (chlorophyll *a*) ranged from close to the detection limit (0.1 μg L^{-1}) to 27.9 μg L^{-1} (Table 3.1). Based on univariate linear regressions, phytoplankton abundance significantly ($P < 0.05$) decreased with surface area, NO_2-N+NO_3–N, DIN:TP ratios and pH and increased with water temperature, TP, SRP and DOC (Appendix 4). Multiple regression analysis identified TP, pH and conductivity as the strongest predictors of phytoplankton abundance in the 28 ponds sampled in 2000 ($\log_{10}$(Chl*a*P + 1) = 2.37 + 0.48 $\log_{10}$TP – 0.44pH + 0.004COND; $P < 0.001$; $r^2 = 0.48$; $P_{TP} = 0.007$; $P_{pH} = 0.004$; $P_{Cond} = 0.020$).

In the 14 ponds sampled in both years, phytoplankton abundance was only slightly higher in 2000 than in 1999 (Table 3.1). In 1999, phytoplankton abundance significantly increased with TP and decreased with DIN:TP ratios and pH (Appendix 5) and multiple regression analysis identified pH and surface area as the strongest predictors ($\log_{10}$(Chl*a*P + 1) = 2.16 – 0.53pH – 0.29$\log_{10}$AREA; $P = 0.009$; $r^2 = 0.50$; $P_{pH} = 0.003$; $P_{area} = 0.021$). In 2000, TP was identified as the only significant predictor of phytoplankton abundance in univariate (Appendix 6) and multiple regression analyses ($\log_{10}$(Chl*a*P + 1) = - 1.22 + 0.88 $\log_{10}$TP; $r^2 = 0.25$; $P = 0.040$).

Phytoplankton community composition – environmental relationships

Based on carotenoid analysis, phytoplankton typically consisted of non-diatom chromophytes (chrysophytes and dinoflagellates; diadinoxanthin, fucoxanthin and Chl *c*) and/or chlorophytes (lutein, Chl *b* and violaxanthin; Figure 3.3). Cyanobacteria (echinenone, canthaxanthin, zeaxanthin and myxoxanthophyll) were usually detectable but were dominant in only two ponds (BML and TP). Diatoms (diatoxanthin) and cryptophytes (alloxanthin) were scarce in the phytoplankton.

RDA of the 28 ponds sampled in 2000 showed that phytoplankton community composition was best predicted by TP, pH and conductivity (Figure 3.4). Together these three variables accounted for 32% of the total variance in the pigment concentrations in the first two RDA axes. The first axis ($\lambda_1 = 0.29$) was significant ($P < 0.01$) and

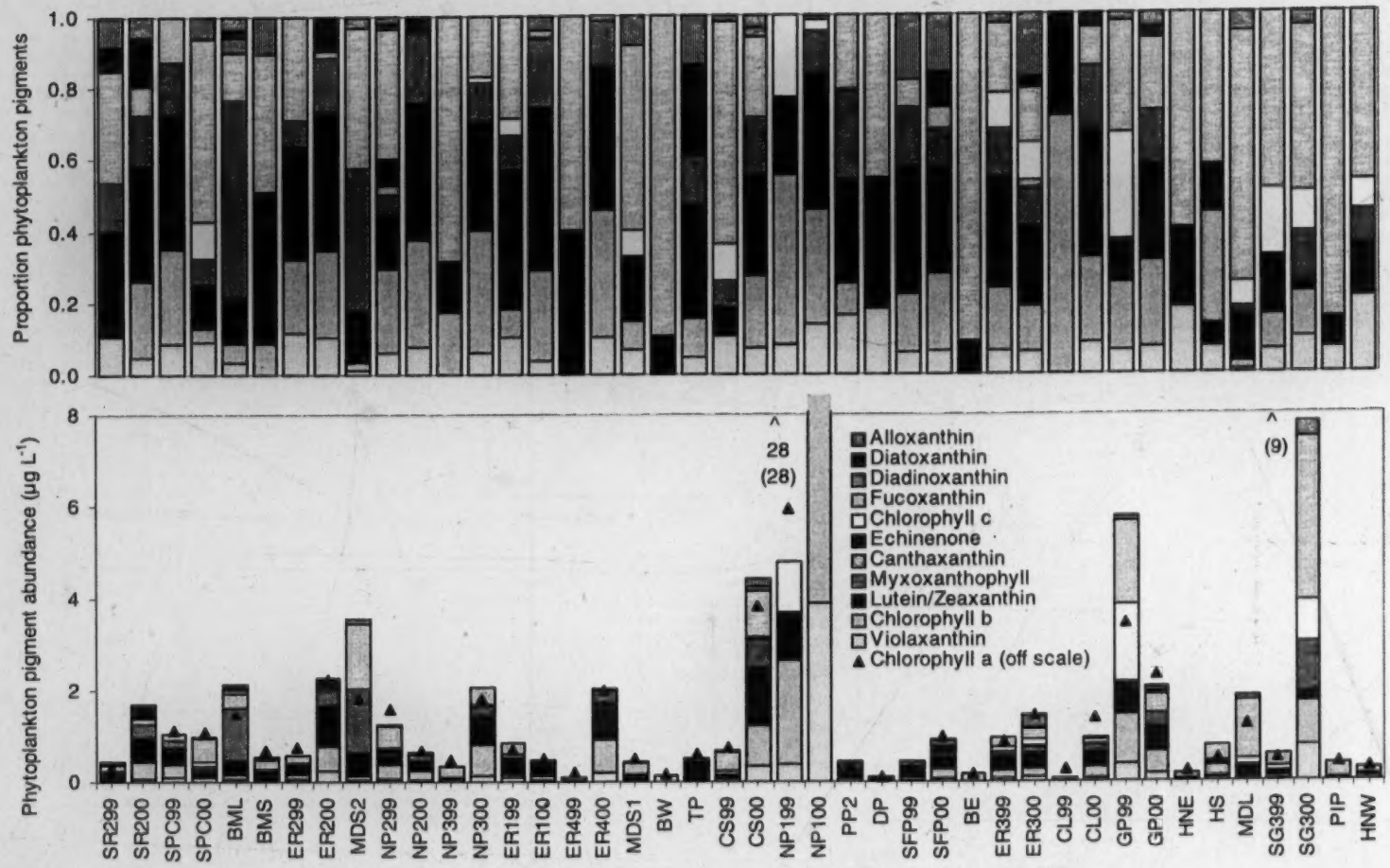


Figure 3.3: Phytoplankton abundance and community composition inferred from pigments from the water column of 28 alpine ponds in Banff National Park at end of July 1999 and/or 2000. Ponds are ordered in increasing depth to the right.

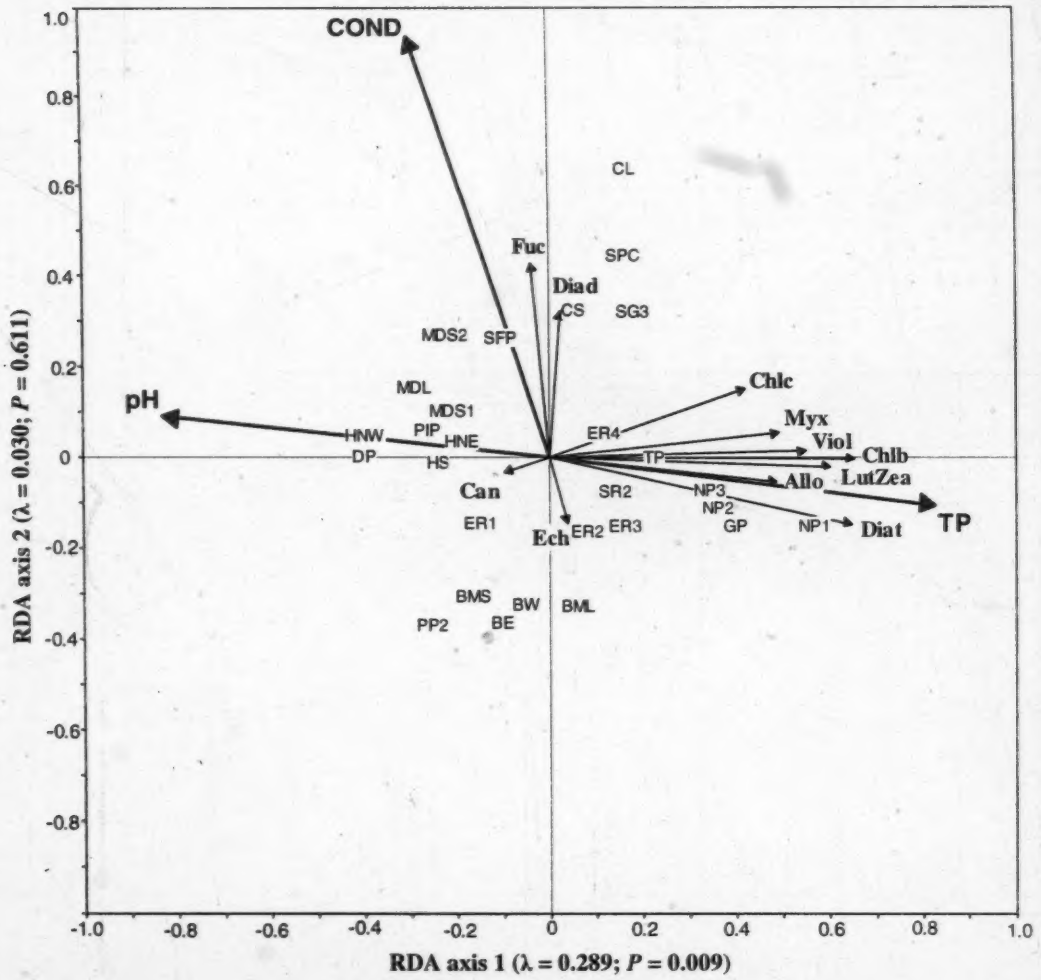


Figure 3.4: Correlation triplot based on partially constrained redundancy analysis representing the influence of total phosphorus, pH and conductivity on phytoplankton community composition as inferred from pigments from 28 ponds sampled in 2000. The first two axes explain 31.9% of the variation in the pigment concentrations. The relative length of an environmental arrow corresponds to the relative importance of that variable explaining the observed variance in the pigment data. The length of a pigment arrow corresponds to its relative importance in the differences across ponds. The placement of arrows relative to other arrows represents their approximate correlation to each other.

represented a gradient of TP and pH, each of which accounted for 9% of the explained variation. The first axis contrasted ponds with high TP concentrations and low pH, which consisted of a mixed community of cryptophytes (alloxanthin), chlorophytes (chl *b*, violaxanthin), chromophytes (chl *c*), diatoms (diatoxanthin) and colonial Cyanobacteria (myxoxanthophyll), from ponds with low TP concentrations and high pH, which contained higher proportions of chromophytes (diadinoxanthin, fucoxanthin) and Cyanobacteria (echinenone, canthaxanthin) (Figure 3.4). Although insignificant, the second axis ($\lambda_1 = 0.03$) represented a conductivity gradient, which captured 3% of the explained variation. Ponds with high conductivity generally had more non-diatom chromophytes (diadinoxanthin, fucoxanthin) and fewer Cyanobacteria (canthaxanthin, echinenone) and diatoms (diatoxanthin) than ponds with low conductivity (Figure 3.4).

RDA of the phytoplankton data from 14 ponds sampled in both 1999 and 2000 indicated that the environmental variables that best predict phytoplankton community composition differed between the two years (Figure 3.5). In 1999, TP, pH and water temperature accounted for 66% of the total variance in the phytoplankton community composition (Figure 3.5). In 2000, none of the environmental variables produced a significant primary axis but the most 'important' (but non-significant variables) did not include any of the three significant variables from 1999 (Figure 3.5).

Epipelon abundance – environmental relationships

In the 28 ponds sampled in 2000, epipelon abundances (chlorophyll *a*) ranged from 0.67 to 39.31 μg cm^{-2} (Table 3.1). NO_2-N+NO_3–N was identified as the only significant predictor of epipelon abundance in univariate (Appendix 7) and multiple regression analyses ($\log_{10}$(Chl*a*E + 1) = 0.53 + 0.30 $\log_{10}$$NO_2$-N+$NO_3$–N; $r^2 = 0.14$; $P = 0.036$).

In the 14 ponds sampled in both years, epipelon abundance was over four times higher in 2000 than in 1999 (Table 3.1). In 1999, epipelon abundance was not related to NO_2-N+NO_3–N ($P = 0.20$) nor to any other environmental feature in univariate (Appendix 8) or multiple regression analysis. In 2000, epipelon abundance significantly increased with DOC and decreased with maximum depth and conductivity (Appendix 9). Multiple

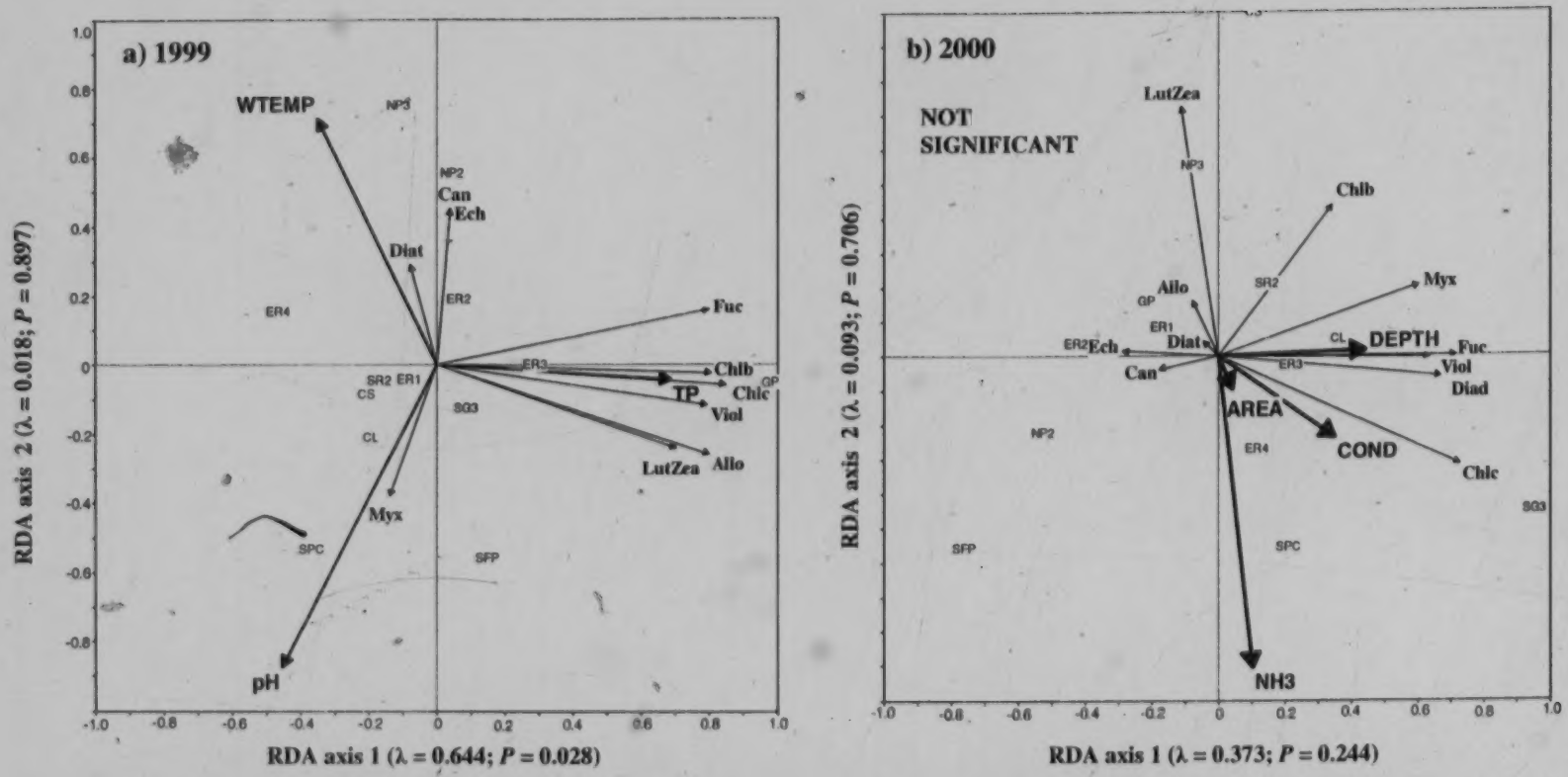


Figure 3.5: Correlation triplots based on partially constrained redundancy analysis on phytoplankton community composition as inferred from pigments from 14 ponds sampled in 1999 (a) and 2000 (b). RDA on 1999 data represents the influence of total phosphorus, pH and water temperature. The first two axes explain 66.2% of the variation in pigment concentrations. RDA on 2000 data was not significant but I include the four most important variables, maximum depth, conductivity, surface area and ammonium concentration. Each axis is labelled with its eigenvalue and *P*-value.

regression analysis identified NO_2-N+NO_3–N, maximum depth and conductivity as the strongest predictors of epipelon abundance in 2000 ($\log_{10}$(Chl*a*E + 1) = 2.01 - 0.01DEPTH + 1.3$\log_{10}$$NO_2$-N+$NO_3$–N + 0.003COND; $P < 0.001$; $r^2 = 0.71$; $P_{depth} = 0.003$; $P_{NO2NO3} = 0.008$; $P_{cond} = 0.008$).

Epipelon community composition – environmental relationships

Epipelon consisted mainly of non-diatom chromophytes (chrysophytes and dinoflagellates) (Figure 3.6). Cyanobacteria and chlorophytes were usually present but in low concentrations. However, Cyanobacteria were dominant in one pond (SR299). Diatoms and cryptophytes made up a larger proportion of the epipelon communities than the phytoplankton communities but were still in low concentrations.

RDA of the 28 ponds sampled in 2000 showed that epipelon community composition was best predicted by NO_2-N+NO_3–N, TP and DOC (Figure 3.7). Together these three variables accounted for 31% of the total variance in the pigment concentrations in the first two RDA axes. The first axis ($\lambda_1 = 0.26$) was significant ($P < 0.02$) and represented a gradient of NO_2-N+NO_3–N and TP, which accounted for 13% and 9% of the explained variation, respectively. The first axis contrasted ponds with high NO_2-N+NO_3–N concentrations and low TP concentrations, which consisted of chromophytes (fucoxanthin) and colonial Cyanobacteria (myxoxanthophyll), from ponds with high TP and low NO_2-N+NO_3–N concentrations, which contained higher proportion of non-colonial Cyanobacteria (echinenone) and chlorophytes (chlorophyll *b*) (Figure 3.7). Although insignificant, the second axis ($\lambda_1 = 0.05$) represented a DOC concentration gradient, which captured 4% of the explained variation. Ponds with high DOC concentration generally had more diatoms (diatoxanthin), cryptophytes (alloxanthin) and chlorophytes (chlorophyll *b*) and fewer Cyanobacteria (myxoxanthophyll, echinenone, canthaxanthin) and non-diatom chromophytes (fucoxanthin, diatoxanthin, chlorophyll *c*) than ponds with low DOC concentration (Figure 3.7).

RDA of the epipelon data from 14 ponds sampled in both 1999 and 2000 identified that the environmental variables that best predict epipelon community composition differed

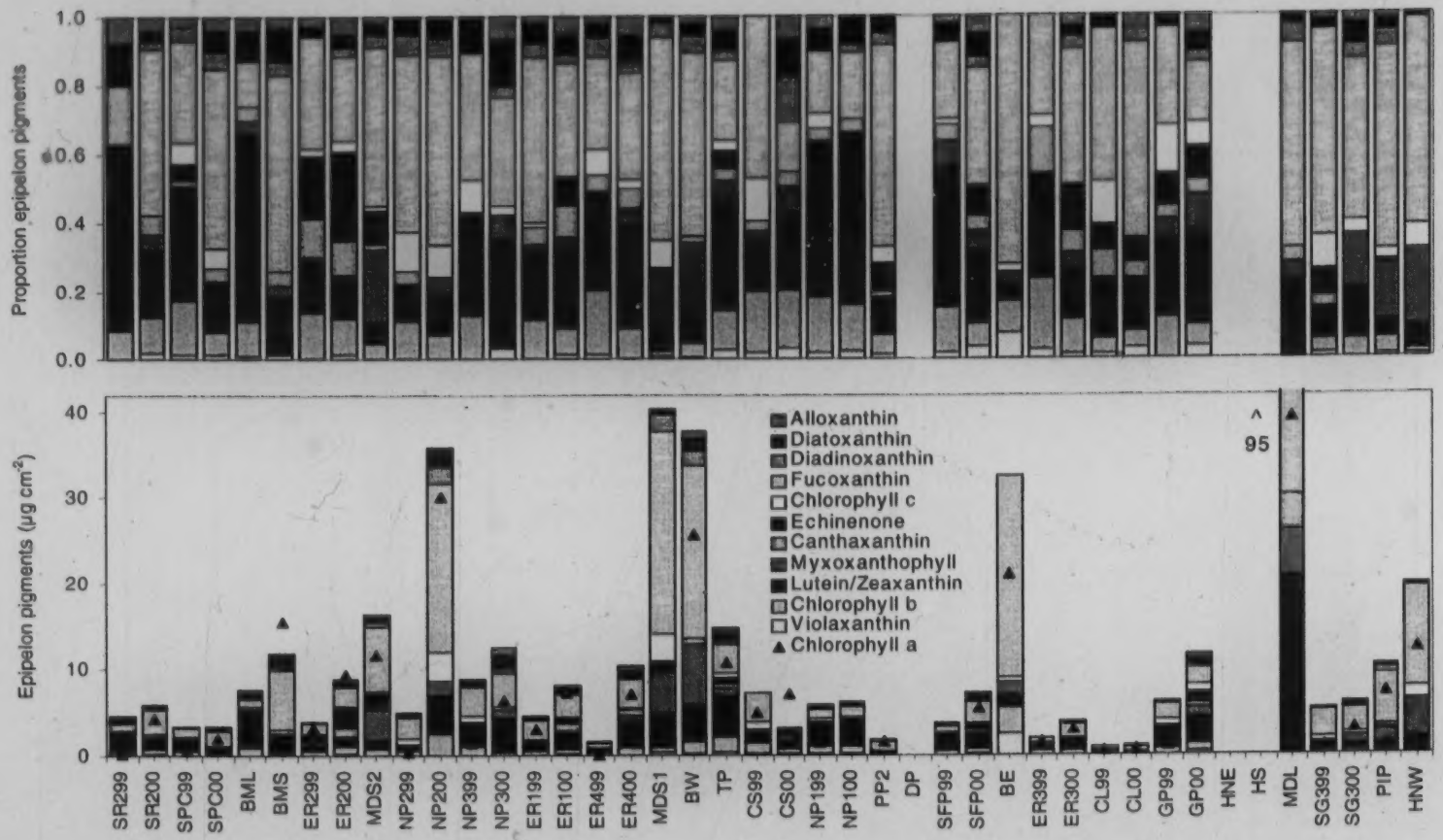


Figure 3.6: Epipelon abundance and community composition inferred from pigments from the sediment of 28 alpine ponds in Banff National Park at end of July 1999 and/or 2000. Ponds are ordered in increasing depth to the right.

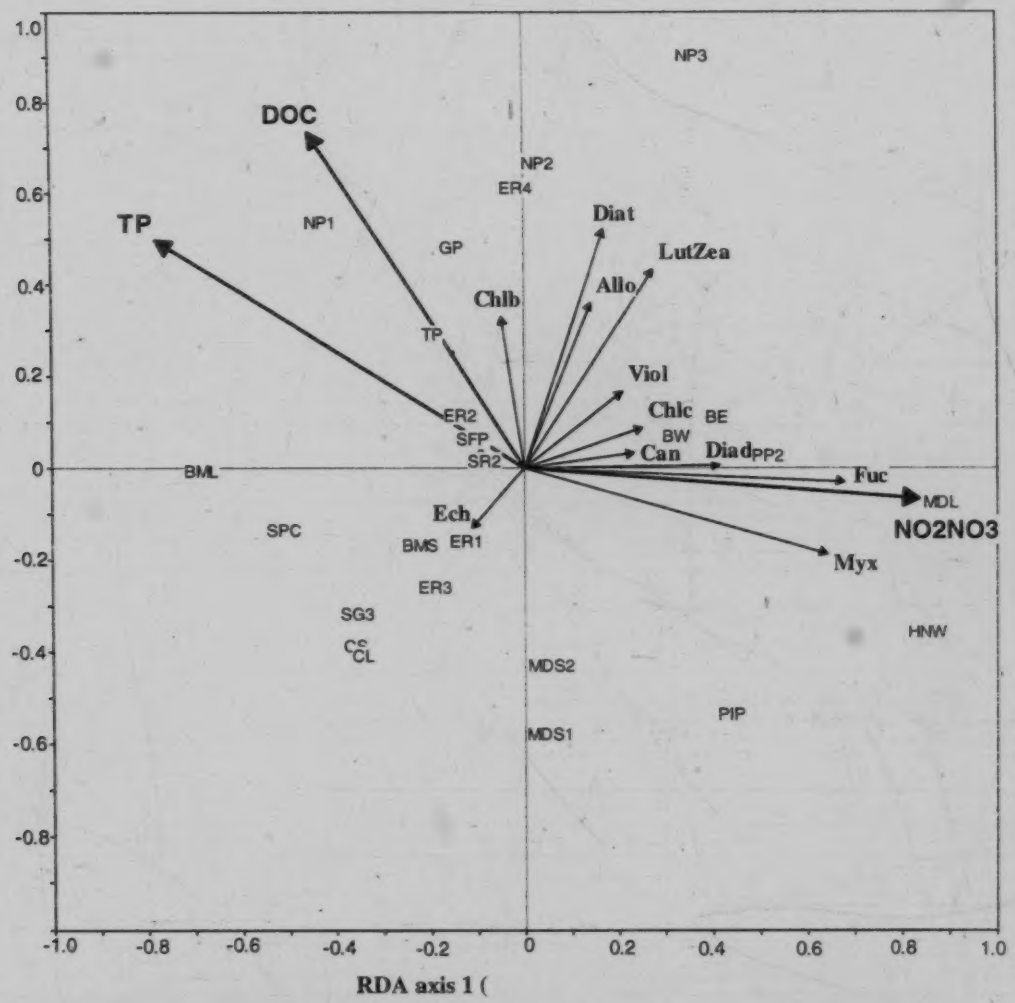


Figure 3.7: Correlation triplot based on partially constrained redundancy analysis representing the influence of nitrite plus nitrate, total phosphorus and dissolved organic carbon concentrations on epipelon community composition as inferred from pigments from 28 ponds sampled in 2000. The first two axes explain 31.0% of the variation in the pigment concentrations. Each axis is labelled with its eigenvalue and p-value.

between the two years (Figure 3.8). In 1999, elevation, pH and conductivity accounted for 40% of the total variance in the epipelon community composition (Figure 3.8). In 2000, water temperature and DOC accounted for 57% of the total variance in the epipelon community composition.

DISCUSSION

Physical and chemical limnology

Based on their basin morphology, the majority of alpine ponds examined in this study represent thrust ponds (Ives 1941). Thrust ponds are typically found in meadows and are characterized by bottoms of fine flocculent organic silt and steep-sided, U-shaped basins formed as a result of ice thrust (Ives 1941). Thrust ponds are also prevalent in the Arctic but called ice-wedge polygons (Hobbie 1980). Dynamic freeze-thaw cycles and water budgets make the basins of thrust ponds quite stable over time (Ives 1941; Hobbie 1980). Thrust ponds may be interconnected but typically lack inflows and outflows and consequently their water budgets depend on precipitation, evaporation and seepage. This dependence makes alpine ponds particularly vulnerable to climate change, similar to arctic ponds (Chapter 2; Douglas and Smol 1994).

Ponds sampled in this study had fairly high DOC concentrations (mean 5.4 mg L^{-1}) in comparison to nearby lakes (< 2.5 mg L^{-1}) (Vinebrooke and Leavitt 1999), probably because the ponds had organic bottoms and higher bottom area to water volume ratios and therefore more autochthonous DOC than lakes. Furthermore, pond catchments had more vegetation and therefore more allochthonous DOC inputs than lakes. DOC concentrations in alpine ponds generally decreased at higher elevations as the amount of vegetation in their catchments decreased, similar to alpine lakes (Vinebrooke and Leavitt 1999). DOC concentrations were lower and likely less aromatic than low elevation lakes. Low DOC concentrations combined with the intense ultraviolet radiation in the alpine altitudes (Blumthaler et al. 1997) and shallow depths of ponds, likely exposes the communities in alpine ponds to high biologically damaging ultraviolet radiation.

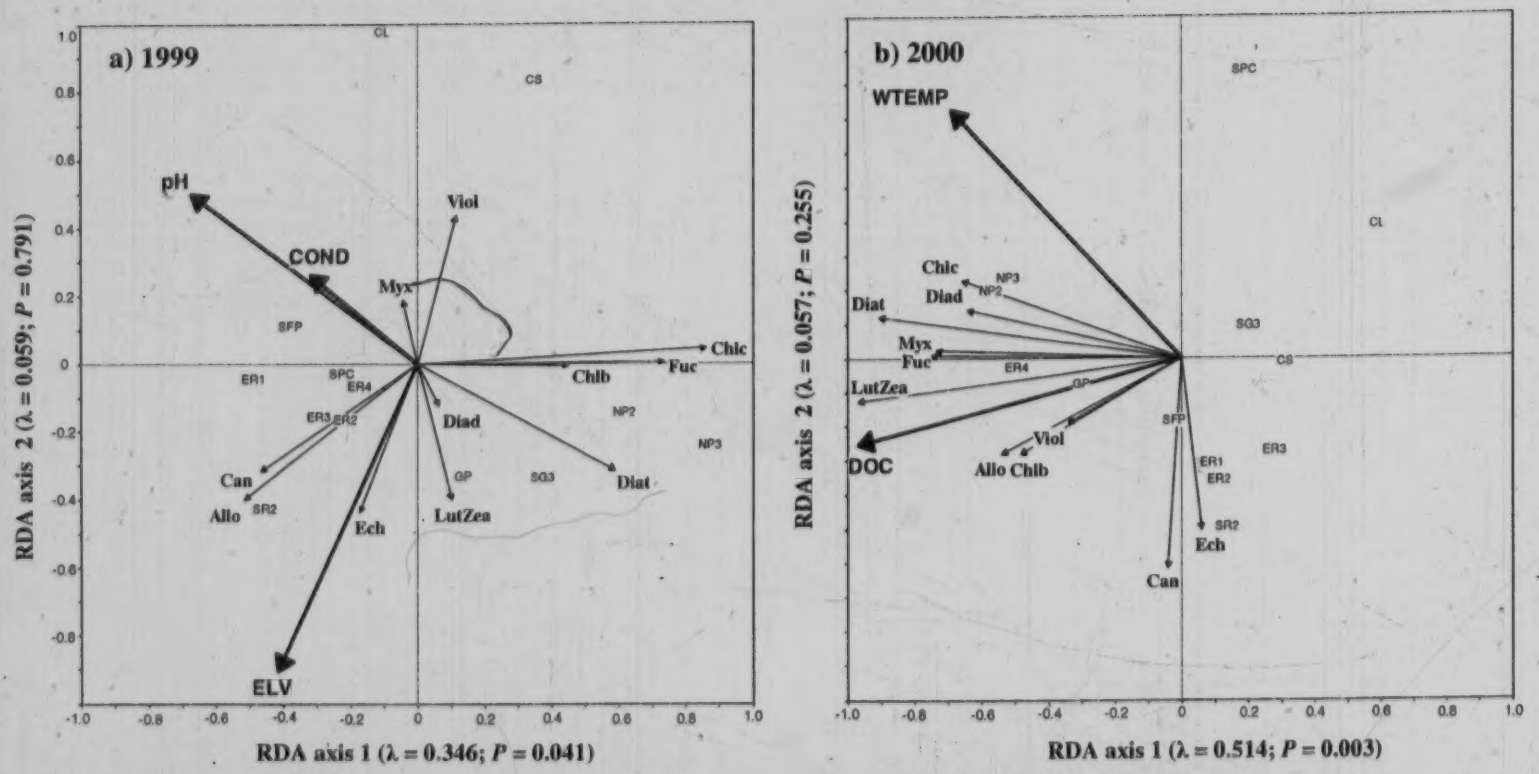


Figure 3.8: Correlation triplots based on partially constrained redundancy analysis on epipelon community composition as inferred from pigments from 14 ponds sampled in 1999 (a) and 2000 (b). RDA on 1999 data represents the influence of pH, conductivity and elevation. The first two axes explain 40.5% of the variation in pigment concentrations. RDA on 2000 data represents the influence of dissolved organic carbon concentration and water temperature. The first two axes explain 57.1% of the variation in pigment concentrations. Each axis is labelled with its eigenvalue and p-value.

Nutrient limitation

Based on DIN:TP ratios, the majority of alpine ponds sampled in Banff National Park were N-limited. This is the first time nutrient limitation has been assessed in North American alpine ponds. In contrast, nutrient limitation has been assessed in numerous mountain lakes throughout the western United States and N-limitation is common (Morris and Lewis 1988; Goldman et al. 1993; Axler and Reuter 1996; Interlandi et al. 1999; Sickman 2001; Lafrançois 2002). Similar to alpine lakes, N-limitation makes alpine ponds particularly susceptible to current increases in atmospheric N deposition (Baron et al. 2000).

Although N-limitation was prevalent, P-limitation did occur, particularly in ponds at high elevations with rock drainage basins. This agrees with other studies that found mountain lakes with steep, rocky watersheds have high N concentrations and N:P ratios, indicative of P-limitation and lakes with gently sloping, vegetated water sheds have high P concentrations and low N:P ratios, indicative of N-limitation (Kopáček et al. 2000; Kamenik et al. 2001). If climate warming stimulates upward tree-line migration and vegetation development, the number of P-limited alpine ponds should decrease.

Algal community composition

Phytoplankton community composition varied greatly across the 28 alpine ponds surveyed, whereas community composition was quite similar across 20 mountain lakes and ponds surveyed using similar methods (Vinebrooke and Leavitt 1999). The opposite was expected given that Vinebrooke and Leavitt's (1999) lakes and ponds were surveyed across an elevation gradient and some systems contained fish, whereas these ponds were all in the alpine and lacked fish. The variability in phytoplankton community composition in alpine ponds may reflect the considerable variability of the physical and chemical features between and within alpine ponds (Chapter 2).

Phytoplankton communities in alpine ponds and nearby mountain lakes and ponds (Vinebrooke and Leavitt 1999) consisted mainly of non-diatom chromophytes and chlorophytes. However, Cyanobacteria were more important in the phytoplankton of

alpine ponds than in nearby mountain lakes and ponds (Vinebrooke and Leavitt 1999). Similar to other mountain lakes and ponds (Vinebrooke and Leavitt 1999) epipelic algal communities in alpine ponds consisted mainly of non-diatom chromophytes. However, epipelic chlorophytes and Cyanobacteria were more important and diatoms were less important in alpine ponds than in other mountain lakes and ponds (Vinebrooke and Leavitt 1999). The dominance of non-diatom chromophytes and chlorophytes in alpine ponds is likely due to the abundance of small species in these groups that typically do extremely well in harsh environments, such as the alpine (Reche et al. 1994; Lafrançois 2002). The occurrence of Cyanobacteria in alpine ponds likely reflects their ability to live in nitrogen-deficient waters that undergo periods of desiccation and intense ultraviolet radiation. However, the sensitivity of Cyanobacteria to rapid shifts in environmental conditions, which occur often in alpine ponds (Chapter 2), likely limits their dominance. The scarcity of diatoms in alpine ponds is likely due to their sensitivity to desiccation (Mosisch 2001) and grazing (Chapter 4) and to silica being below or close to limitation concentrations (< 0.5 mg L^{-1}).

Phytoplankton abundance and community composition - environmental relationships

TP, pH and conductivity were the main environmental gradients that control phytoplankton abundance and community composition in the 28 alpine ponds surveyed in 2000. These findings contrast those of Vinebrooke and Leavitt (1999) who sampled mountain lakes and ponds in Banff National Park using similar methods. They found phytoplankton abundance was explained by none of the environmental variables measured and phytoplankton community composition was best explained by zooplankton biomass, elevation and DOC (Vinebrooke and Leavitt 1999). However, similar to this study they found that conductivity was an important environmental gradient (Vinebrooke and Leavitt 1999). The differences between results probably occurred because I did not sample zooplankton and all these ponds were located in the alpine rather than along an elevation gradient. Although similar DOC concentration gradients were sampled in both studies, montane and subalpine lakes sampled by Vinebrooke and Leavitt (1999) likely had more aromatic DOC (McKnight et al. 2001) than alpine ponds. Therefore, their DOC

concentration gradient likely represents a larger ultraviolet radiation attenuation gradient than ours.

Phytoplankton abundance and the abundance of most algal groups in alpine ponds were positively related to water column TP. This is consistent with low elevation lakes (McCauley et al. 1989; Prairie et al. 1989; Watson et al. 1997). Non-diatom chromophytes, such as chrysophytes, were unrelated to water column TP in alpine ponds. Others have also found that abundance of chrysophytes was unrelated to TP and that chrysophytes typically do well in low nutrient environments with high N:P ratios (Sandgren 1988; Watson et al. 1997). The negative relationship between TP and non-colonial Cyanobacteria was negligible and not considered further.

Water column pH was also a significant predictor of phytoplankton abundance and community composition in alpine ponds. As pH decreased, overall abundance and abundance of most phytoplankton groups increased. It is important to note that my pH gradient was neutral to alkaline (6.4 - 8.4); therefore the community composition shifts relative to pH should be different from community shifts expected along an acidic pH gradient (Findlay et al. 1999). The negative relationship between pigment abundances and pH is likely related to the negative relationship between pH and TP and to the effect of pH on nitrogen availability (Wetzel 2001). NH_4^+ should decrease as pH increases and since algae in alpine ponds are likely N-limited and NH_4^+ is likely their preferred N source, it was expected that phytoplankton abundance would decrease as pH increased.

Consistent with results from other montane ponds and lakes (Vinebrooke and Leavitt 1999), conductivity was a significant predictor of phytoplankton abundance and community composition in alpine ponds. In other studies the relationship between conductivity and algal abundance has been attributed to conductivity being a surrogate measure of inorganic nutrient availability (Vinebrooke and Leavitt 1999) but I have no evidence to confirm this.

Epipelon abundance and community composition - environmental relationships

In the 28 alpine ponds surveyed, epipelon abundance was best explained by NO_2-N+NO_3–N and epipelon community composition was best explained by TP and DOC in addition to NO_2-N+NO_3–N. In contrast, Vinebrooke and Leavitt (1999) found that epipelon abundance in mountain lakes and ponds was best explained by DOC and community composition was explained by none of the environmental variables measured. They attributed their weak epipelon-environmental relationship to the importance of substratum or algal mat chemistry instead of water column chemistry in regulating nutrient availability in montane lakes (Vinebrooke and Leavitt 1999). Conversely, my strong epipelon-environmental relationship reflects the importance of water column chemistry in addition to sediment chemistry for epipelon in these shallow alpine ponds. The boundary between the water column and sediment is less distinct in shallow lakes and ponds because sediment and epipelon are being constantly suspended into the water column (Chapter 2; Alexander et al. 1980; Scheffer 1998).

Similar to other N-limited systems (Lafrançois 2002), epipelon abundance in alpine ponds increased significantly with water column NO_2-N+NO_3–N. This further suggests that epipelon rely on water column nutrients in addition to nutrients from the sediment. Both N and P were significant predictors of epipelon community composition in alpine ponds. N and P were inversely related therefore shifts in epipelon communities can be related to changes in the N:P ratios as well as individual nutrient concentrations. Based on the resource-ratio theory (Smith and Bennett 1999) and results from nutrient enrichment experiments in alpine ponds (Chapter 4) I expected N-fixing Cyanobacteria to thrive in low N and high P environments (low N:P) and chlorophytes and chromophytes to thrive in high N and low P environments (high N:P). I did find that non-colonial Cyanobacteria were common at low N:P and chromophytes were common at high N:P but in contrast to what was expected, chlorophytes were common at low N:P and colonial Cyanobacteria were common at high N:P. Chlorophytes usually have a high N optimum (Sandgren 1988) and flourish at high N:P however many of the chlorophytes species present in alpine ponds are small with large surface area:volume ratios (McMaster unpublished data) thus do well in low nutrient environments (Sandgren 1988). Most

colonial Cyanobacteria taxa found in these ponds are not capable of N-fixing and therefore likely to be N-limited.

Water column DOC was a significant predictor of epipelon community composition in alpine ponds. Much of the response to DOC can be explained by its correlation to TP and NO_2-N+NO_3–N and by the ability of DOC to attenuate photosynthetically active radiation (PAR) and biologically damaging ultraviolet radiation (UVR) (Scully and Lean 1994). Epipelon communities in alpine ponds with higher DOC concentrations and therefore low PAR and UVR, generally had more diatoms (diatoxanthin), cryptophytes (alloxanthin) and chlorophytes (chlorophyll *b*) and fewer Cyanobacteria (myxoxanthophyll, echinenone, canthaxanthin) and non-diatom chromophytes (fucoxanthin, diatoxanthin, chlorophyll *c*) than ponds with lower DOC concentrations and therefore high PAR and UVR. Most diatom taxa are sensitive to UVR because they are unable to efficiently produce photoprotective pigments (Roy 2000) and they have a poor capacity for repair after UVR damage (Queada and Vincent 1997). In contrast, most Cyanobacteria are able to withstand high UVR because they are able to produce photoprotective pigments (Roy 2000) and have a good repair capacity (Queada and Vincent 1997). Cryptophytes and many forms of chlorophytes do very well in low PAR conditions and therefore high DOC concentrations (Klug and Cottingham 2001). Non-diatom chromophytes, such as chrysophytes and dinoflagellates, can actively avoid UVR and consequently flourish in low DOC systems (Vinebrooke and Leavitt 1999). In other respects, my results were inconsistent with previous work. Vinebrooke and Leavitt (1998) found epipelon in alpine lakes were unresponsive to DOC because most taxa were capable of active avoidance of UVR. Furthermore, they found that epilithic Cyanobacteria in mountain ponds and lakes increase with DOC and they attributed this to Cyanobacteria's heterotrophic metabolism (Vinebrooke and Leavitt 1999). In alpine ponds, water column DOC is probably not a main carbon source for the epipelon because the bottom sediment should receive abundant carbon and the bottom should have sufficient PAR.

Interannual variability in the algal - environmental relationships

The physical and chemical variables that best predict phytoplankton and epipelon abundance and community composition in 14 alpine ponds differed between two summers. Interannual variability in phytoplankton-environmental relationships was also documented in high mountain lakes in Spain (Villar-Argaiz et al. 2001). As I found, their interannual variability in relationships coincided with significant changes in the environmental variables between years (Villar-Argaiz et al. 2001). In my ponds, surface area decreased and NH_4-N, DIN, TP and pH increased significantly as precipitation amounts decreased significantly and temperatures increased slightly in 2000. Similarly, interannual fluctuations of primary production in subalpine lakes were linked to precipitation amounts (Goldman et al. 1989). Interannual variability in algal-environmental relationships may also have resulted from changes in the environmental variables not measured, such as grazing. Grazers can alter community composition and impact available nutrient stoichiometry and therefore changes in grazer abundance or composition could have direct and indirect effects on the algal-environmental relationships. However, because my results are correlation based, experiments are needed to confirm if the algal-environmental relationships actually change interannually and determine the drivers of these changes.

Summary

These results suggest that algal communities in alpine ponds are controlled by different physical and chemical variables than nearby mountain lakes and ponds (Vinebrooke and Leavitt 1999). Yet similar to Vinebrooke and Leavitt's (1999) results, my results suggest that algal communities in alpine ponds may be sensitive to climate change. The chemical variables that I found to best predict patterns in phytoplankton and epipelon abundance and community composition in alpine ponds, such as pH, conductivity, and DOC, have been linked to changes in climate in alpine ponds (Chapter 2) or other systems (Psenner and Schmidt 1992; Schindler et a. 1996). However, because I found major interannual variability in the environmental-algal relationships I will not make predictions on how the algal communities will respond to environmental change. I believe that it is necessary to

have several years of data to generate realistic predictive models for the future or deductive models about the past.

REFERENCES

Alexander, V., Stanley, D.W., Daley, R.J. and McRoy, C.P. 1980. Primary Producers. *In* Limnology of Tundra Pond. *Edited by* J.E. Hobbie. Dowden, Hutchinson and Ross, Inc., Pennsylvania, USA pp. 179-250.

Anderson, M.J. and Gribble, N.A. 1998. Partitioning the variation among spatial, temporal and environmental components in a multivariate dataset. Australian Journal of Ecology **23**: 158-167.

Anderson, R.S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in Western Canada. Journal of Fisheries Research Board of Canada **28**: 311-321.

Anderson, R.S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. Journal of the Fisheries Research Board of Canada **31**: 855-869.

Axler, R.P. and Reuter, J.E. 1996. Nitrate uptake by phytoplankton and periphyton: Whole lake enrichment and mesocosm ^{15}N experiment in an oligotrophic lake. Limnology and Oceanography **41**: 659-671.

Baron, J.A., Rueth, H.M., Wolfe, A.M., Nydick, K.R., Allstott, E.j., Minear, J.T. and Moraska, B. 2000. Ecosystem response to nitrogen deposition in the Colorado Front Range. Ecosystems **3**: 352-368.

Beder, K. 1967. Ecology of the alpine vegetation of Snow Creek Valley, Banff National Park, Alberta. M.Sc. thesis, University of Calgary. Calgary, Alberta, Canada.

Bennion, H. and Smith, M.A. 2000. Variability in the water chemistry of shallow ponds in southeast England, with special reference to the seasonality of nutrients and implications for modeling trophic status. Hydrobiologia **436**: 145-158.

Blumthaler, M.W., Ambach, W. and Ellinger, R. 1997. Increase in solar UV radiation with altitude. Journal of Photochemistry and Photobiology **39**: 130-134.

Bowman, W.D. 2000. Biotic controls over ecosystem response to environmental change in alpine tundra of the Rocky Mountains. Ambio **29**: 396-400.

Douglas, M.S.V. and Smol, J.P. 1994. Limnology of high arctic ponds (Cape Herschel, Ellesmere Island, N.W.T.). Archiv für Hydrobiologie **131**: 401-434.

Environment Canada. 2002. Database for Banff Town Site available through Environment Canada's Meteorological Service of Canada. http://www.msc-smc.ec.gc.ca/climate/station_catalogue/index_e.cfm

Findlay, D.L., Kasian, S.E.M., Turner, M.T. and Stainton, M.P. 1999. Responses of phytoplankton and epilithon during acidification and early recovery of a lake. Freshwater Biology **42**: 159-175.

Fyfe, J.C. and Flato, G.M. 1999. Enhanced climate change and its detection over the Rocky Mountains. Journal of Climate **12**: 230-243.

Giorgi, F., Hurrell, J.W. and Marinucci, M.R. 1997. Elevation dependency of the surface climate change signal: A model study. Journal of Climate **10**: 288-296.

Goldman, C.R., Jassby, A. and Powell, T. 1989. Interannual fluctuations in primary production: Meteorological forcing at two subalpine lakes. Limnology and Oceanography **34**: 310-323.

Goldman, C.R., Jassby, A.D. and Hackley, S.H. 1993. Decadal, interannual and seasonal variability in enrichment bioassays at Lake Tahoe, California-Nevada, USA. Canadian Journal of Fisheries and Aquatic Sciences **50**: 1489-1496.

Hauer, F.R., Baron, J.S., Campbell, D.H., Fausch, K.D., Hostetler, S.W., Leavesley, S.W., Leavitt, P.R., McKnight, D.M. and Stanford, J.A. 1997. Assessment of climate change and freshwater ecosystems of the Rocky Mountains, US and Canada. Hydrological Processes **11**: 903-924.

Hobbie, J.E. 1980. Limnology of Tundra Ponds: Barrow Alaska. Dowden, Hutchinson and Ross, Inc., Pennsylvania, USA.

Interlandi, S.J., Kilham, S.S. and Theriot, E.C. 1999. Response of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. Limnology and Oceanography **44**: 668-682.

Ives, R.L. 1941. Tundra Ponds. Journal of Geomorphology **4**: 285-296.

Jeffrey, S.W., Mantoura, R.F.C. and Wright, S.W. 1997. Phytoplankton pigments in oceanography. UNESCO publishing, Paris.

Kamenik, C., Schmidt, R., Kum, G. and Psenner, R. 2001. The influence of catchment characteristics of the water chemistry of mountain lakes. Arctic, Antarctic and Alpine Research **33**: 404-409.

Klug, J.L. and Cottingham, K.L. 2001. Interactions among environmental drivers: Community responses to changing nutrients and dissolved organic carbon. Ecology **82**: 3390-3403.

Kopáček, J., Stuchlík, E., Straškrabová, V. and Pšenáková, P. 2000. Factors governing nutrient status of mountain lakes in the Tatra Mountains. Freshwater Biology **43**: 369-383.

Lafrançois, B.M. 2002. Algal and invertebrate response to atmospheric nitrogen deposition in Rocky Mountain lakes. Ph.D. thesis, Colorado State University, Fort Collins, Colorado, United States.

McCauley, E., Watson, S.B. and Downing, J.A. 1989. Sigmoid relationships between nutrients and chlorophyll among lakes. Canadian Journal of Fisheries and Aquatic Sciences **46**: 1171-1175.

McKnight, D.M., Boyer, E.W., Doran, P., Westerhoff, P.K., Kulbe, T. and Andersen, D.T. 2001. Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. Limnology and Oceanography **46**: 38-48.

Morris, D.P. and Lewis, W.M. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biology **20**: 315-327.

Mosisch, T.D. 2001. Effects of desiccation on stream epilithic algae. New Zealand Journal of Marine and Freshwater Research **35**: 173-179.

Neldner, K.N. and Pennak, R.W. 1955. Seasonal faunal variations in a Colorado alpine pond. American Midland Naturalist **53**: 419-430.

Prairie, Y.T., Duarte, C.M. and Klaff, J. 1989. Unifying nutrient-chlorophyll relationships in lakes. Canadian Journal of Fisheries and Aquatic Sciences **46**: 1172-1182.

Psenner, R. and Schmidt, R. 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. Nature **356**: 781-783.

Quesada, A. and Vincent, W.F. 1997. Strategies of adaptation by Antarctic Cyanobacteria to ultraviolet radiation. European Journal of Phycology **32**: 335-342.

Reche, I., Sachez-Castillo, P. and Carrillo, P. 1994. The principle regulating mechanism on the structure of the phytoplankton community in a high mountain lake. Archiv für Hydrobiologie **130**: 163-178.

Rosemond, A.D., Mulholland, P.J. and Brawley, S.H. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients and herbivores. Canadian Journal of Fisheries and Aquatic Sciences **57**: 66-75.

Roy, S. 2000. Strategies for the minimization of UV-induced damage. *In* The Effects of UV Radiation in Marine Ecosystems. *Edited by* S. deMora, S. Demers and M. Vernet. Cambridge University Press, Cambridge, UK pp. 177-205.

Sandgren, C.D. 1988. The ecology of Chrysophyte flagellates: Their growth and perennation strategies as freshwater phytoplankton. *In* Growth and reproductive strategies of freshwater phytoplankton. *Edited by* C.D. Sandgren. Cambridge University Press, Cambridge, UK pp.9-104.

Scheffer. M. 1998. Ecology of Shallow Lakes. Chapman and Hall, London.

Schindler, D.W., Bayley, S.E. and Parker, B.R. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, Northwestern Ontario. Limnology and Oceanography **41**: 1004-1017.

Schmitz, E.H. 1959. Seasonal biotic events in two Colorado alpine tundra ponds. The American Midland Naturalist **61**: 424-445.

Scully, N.M. and Lean, D.R.S. 1994. The attenuation of ultraviolet radiation in temperate lakes. Archiv für Hydrobiologie Beihefte Ergebnisse der Limnologie **43**:134-144.

Sickman, J.O. 2001. Comparative analysis of nitrogen biogeochemistry in high elevation ecosystems. Ph.D. thesis, University of California, Santa Barbara, California, United States.

Smith, V.H. and Bennett, S.J. 1999. Nitrogen:phosphorus supply ratios and phytoplankton community structure in lakes. Archiv für Hydrobiologie **146**: 37-53.

Smol, J.P. and Cumming, B.F. 2000. Tracking long-term changes in climate using algal indicators in lake sediments. Journal of Phycology **36**: 986-1011.

STATISTICA. 1998. StatSoft, Inc. Tulsa, Oklahoma.

ter Braak, C.J.F. and Smilauer, P. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: Software for Canonical community ordination (version 4). Microcomputer Power, Ithaca, New York, United States.

Villar-Argaiz, M., Medina-Sanchez, J.M. and Cruz-Pizarro, L. 2001. Inter- and intra-annual variability in the phytoplankton community of a high mountain lake: the influence of external (atmospheric) and internal (recycled) sources of phosphorus. Freshwater Biology **46**: 1017-1034.

Vinebrooke, R.D., Dixit, S.S., Graham, M.D., Gunn, J.M., Chen, Y. and Belzile, N. 2002. Whole-lake algal responses to a century of acidic industrial deposition on the Canadian Shield. Canadian Journal of Fisheries and Aquatic Sciences **59**: 483-493.

Vinebrooke, R.D. and Graham, M.D. 1997. Periphyton assemblages as indicators of recovery in acidified Canadian Shield lakes. Canadian Journal of Fisheries and Aquatic Sciences **54**: 1557-1568.

Vinebrooke, R.D. and Leavitt, P.R. 1998. Direct and interactive effects of allochthonous dissolved organic matter, inorganic nutrients and ultraviolet radiation on an alpine littoral food web. Limnology and Oceanography **43**: 1065-1081.

Vinebrooke, R.D. and Leavitt, P.R. 1999. Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. Journal of North American Benthological Society **18**: 14-32.

Watson, S.B., McCauley, E. and Downing, J.A. 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. Limnology and Oceanography **42**: 487-495.

Wetzel, R. 2001. Limnology: Lake and river ecosystems. Academic Press, San Diego, United States.

Williams, M.W., Baron, J.S., Caine, N., Sommerfeld, R. and Sanford, R. 1996. Nitrogen saturation in the Rocky Mountains. Environmental Science and Technology **30**: 640-646.

Wolfe, A.P., Baron, J.S. and Cornett, R.J. 2001. Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). Journal of Paleolimnology **25**: 1-7.

Zar, J.H. 1999. Biostatistical Analysis. Prentice Hall, New Jersey, United States.

CHAPTER 4: TEMPORAL EFFECTS OF NUTRIENT (N,P) ENRICHMENT AND INVERTEBRATE GRAZING ON EPILITHIC ALGAL ABUNDANCE AND COMMUNITY STRUCTURE IN ALPINE PONDS OF THE CANADIAN ROCKIES

INTRODUCTION

Atmospheric nitrogen (N) has increased regionally as a result of human activities such as fossil fuel combustion and fertilizer application (Vitousek et al. 1997). In the Colorado Rocky Mountains, N deposition has doubled or tripled in the last two decades (Williams et al. 1996a; Baron et al. 2000). Increasing N deposition also seems to be beginning in Alberta, for example annual wet nitrate deposition has increased from under 1.7 to over 2.4 kg ha^{-1} yr^{-1} over the last 15 years in Kananaskis Country (1403 meters above sea level; Alberta Environment 2003). Alpine aquatic ecosystems are particularly sensitive to increased atmospheric N deposition because their steep, sparsely vegetated watersheds readily transport nitrate and their waters are intrinsically low in N (Williams et al. 1996a; Sickman 2001). Increased atmospheric N loading has been linked to eutrophication in N-limited subalpine and alpine lakes in the western United States (Baron et al. 2000; Wolfe et al. 2001). However, no experiments have been conducted in alpine systems in the Canadian Rocky Mountains. A recent survey of 28 alpine ponds in Banff National Park found that the majority of ponds had extremely low ambient nitrogen to phosphorus ratios (Chapter 3), indicative of N-limited algal growth (Morris and Lewis 1988). In this study I used nutrient diffusing substrates to experimentally test whether epilithic algae in alpine ponds are N-limited and therefore responsive to increased atmospheric N loading.

Although nutrients are often the prime determinant of algal abundance, the response to nutrient enrichment can be masked by herbivores because of consumption of biomass, recycling of nutrients and shifts in species composition (Feminella and Hawkins 1995; Steinman 1996). The relative importance of herbivory and nutrient enrichment in controlling a benthic algal community depends on factors such as algal edibility (Rosemond et al. 1993), herbivore type (Leibold and Wilbur 1992) and food web length (Oksanen et al. 1981; Carpenter et al. 1987; Brett and Goldman 1997). A community may, for example, be controlled more by herbivory than by nutrient availability when

algae are edible and/or herbivores have few competitors or predators. In contrast a community may be controlled more by nutrient availability than herbivory when algae are grazer-resistant and/or herbivores have many competitors or predators (Rosemond et al. 1993). The impact of benthic herbivores and the relative importance of nutrient availability and herbivory in controlling benthic algal communities in alpine ponds are unknown. Understanding this interaction is essential because herbivores can obscure the response of algal abundance and community composition to nutrient enrichment (Peterson et al. 1993; Rosemond et al. 1993; Hillebrand and Kahlert 2001).

Individual and interactive effects of nutrient enrichment and herbivory may change seasonally as ambient nutrient concentrations and herbivore densities change through time (Rosemond et al. 2000; Hillebrand and Kahlert 2001; Peterson et al. 2001). For instance, in a Tennessee stream both herbivory and nutrient availability remained limiting throughout the year but grazing by snails was relatively more important than nutrient availability in spring, whereas nutrient availability was relatively more important than grazing in summer and fall (Rosemond et al. 2000). These differences were attributed to low grazer densities and high nutrient concentrations in the spring (Rosemond et al. 2000). It is therefore important to experiment through the ice-free season in order to determine if and how the controls vary seasonally.

The aim of this study was to determine the temporal effect of N deposition on epilithic algae in alpine ponds and how herbivory might modify the response to N. The specific objectives were: 1) to determine whether epilithon abundance and community composition in pristine alpine ponds respond to nitrogen inputs (i.e., N-limitation), 2) to determine whether the nutrient effects depend on grazing pressure (i.e., nutrient-grazer interaction) and 3) to determine whether the individual and interactive nutrient and grazer effects are time-dependent over the ice-free season. To address these objectives I experimentally manipulated nutrients and grazers in early and mid-summer in three alpine ponds in Banff National Park, Canada.

METHODS

Study site

The study ponds are located on Snow Creek Summit (2300 m above sea level; 51°36'N, 115° 51'W) in the eastern front ranges of the Rocky Mountains in Banff National Park, Alberta, Canada (Figure 4.1). Pond catchments consist of a mosaic of small patches of exposed sedimentary rock, including limestone, shale and sandstone, and sparsely vegetated pockets of orthic eutric brunisols (Holland and Coen 1982). Vegetation on sites with soils includes white heather (*Cassiope tetragona*), yellow heather (*Phyllodoce glanduliflora*), arctic willow (*Salix arctica*), white mountain avens (*Dryas hookeriana*), bladder locoweed (*Oxytropis podocarpa*), sedges (*Carex* spp.), lichens, kruppelholz Engelmann spruce (*Picea engelmannii*) and kruppelholz alpine fir (*Abies lasiocarpa*) (Beder 1967).

The three ponds are located within 670 m of each other. East Ridge One (ER1) is relatively small (0.021 ha, maximum depth 0.38 m), East Ridge Three (ER3) is somewhat larger (0.058 ha, maximum depth 0.94 m) and Snowflake Pond (SFP) is much larger (0.142 ha, maximum depth 0.54 m). All ponds lack inflows. ER1 and ER3 have outflows that flow only during high water levels. Snowmelt dominates pond hydrology and water levels usually decline during the ice-free season that extends from early June to late September. Daily pond water temperatures follow air temperature and range from 0.3 to 33 °C in the ice-free season. Pond bottoms consist of unconsolidated organic sediment and scattered rocks. Ponds freeze solid in the winter and lack fish and macrophytes.

Experimental Design

I used a three-factor design to test the independent and interactive effects of nutrients (ambient, plus P, plus N and plus N and P), grazers (ambient and reduced) and time (early summer and mid-summer) on epilithic algal abundance and community structure. This design resulted in 16 different treatment combinations. ER1, ER3, the west end of SFP and the east end of SFP each received one set of the 16 treatment combinations. Replication was undertaken in SFP to account for increased variation expected across this

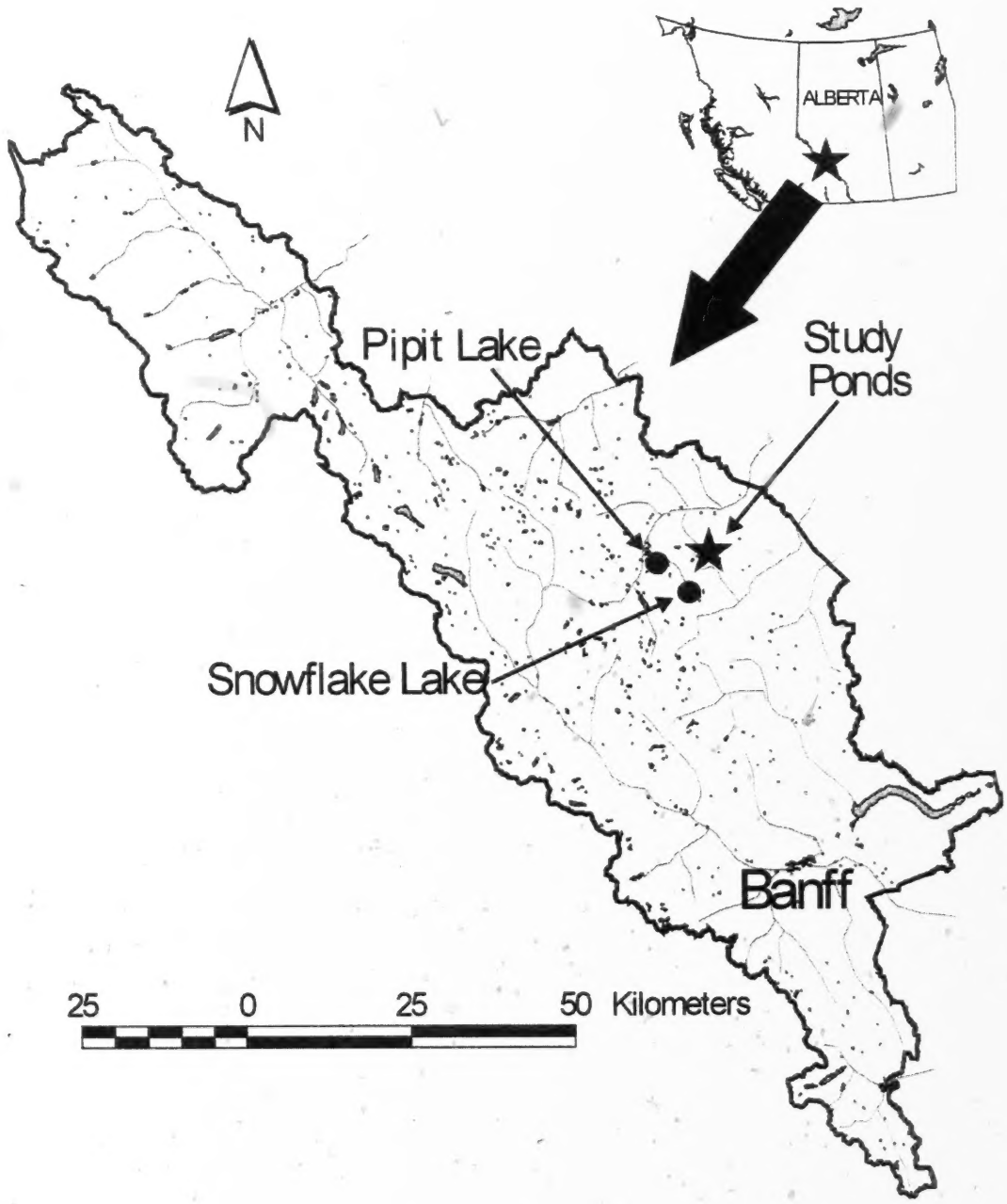


Figure 4.1: Study ponds are located on Snow Creek Summit (51°36'N, 115° 51'W) in Banff National Park, Alberta, Canada.

large pond. However, samples from the west and east ends of SFP were pseudoreplicates and therefore averaged before statistical analysis.

Nutrient treatments were achieved using nutrient diffusion substrates (NDS). NDS construction followed Scrimgeour and Chambers (1997) who determined nutrient release rates for the type of NDS I employed. They estimated that with 0.5 M $NaNO_3$ and 0.5 M KH_2PO_4, nutrient release rates decreased at a log-linear rate over a 31 day period from over 5000 μmol NO_3-N l^{-1} d^{-1} and 3500 μmol PO_4-P l^{-1} d^{-1} to under 200 μmol NO_3-N and 200 μmol PO_4-P l^{-1} d^{-1}. Each NDS consisted of a commercially available ribbed, clay flowerpot (11 cm diameter, 6 cm high, 325 ml volume), a polypropylene base (12 cm diameter, 4 mm thick) and two strands of nylon cord. To pre-clean the substrata, new pots were soaked in deionized distilled water for 25 days. Pots were oven dried and filled either with 2% agar (control), 2% agar and 0.5 M KH_2PO_4 (plus P), 2% agar and 0.5 M $NaNO_3$ (plus N), or 2% agar, 0.5 M $NaNO_3$ and 0.5 M KH_2PO_4 (plus N and P). Pots were sealed with a polypropylene base using a silicone that did not release nutrients. The NDS were stored in airtight plastic bags at 4 °C in the dark for less than one week before deployment.

Grazer treatment (ambient and reduced) was achieved by placing NDS representing each nutrient treatment (control, plus P, plus N, plus N and P) on the pond bottom or suspended 0.1 m below the water surface. Suspended NDS should be inaccessible to caddisfly and snail colonization while maintaining the physical environment surrounding the NDS (Lamberti and Resh 1983) and allowing algal colonization (Hoagland et al. 1986). All NDS were separated by $\geq$ 1 m to minimize nutrient treatment interactions.

Time treatment (early summer and mid-summer) was achieved by conducting the five-week nutrient-grazer experiment at the beginning (June 19 to July 22 in ER1 and ER3 and June 20 to July 24 in SFP) and middle (July 24 to August 26 in ER1 and ER3 and July 26 to August 30 in SFP) of the ice-free season. The time treatment allowed us to account for temporal variation in ambient nutrient concentrations and grazer densities.

Sampling protocol and analyses

During each five-week incubation period I measured numerous physical, chemical and biological variables in each pond. Water temperature was recorded hourly with an Onset Hobo® temperature logger installed 0.1m below the water surface in each pond. Twice weekly, snails and caddisflies were counted on the NDS, conductivity was measured with a Cole-Parmer® handheld TDSTestr 40 with automatic temperature correction and depths of the NDS below the water surface were measured and adjusted as necessary to maintain their position at 0.1 m below the surface.

Phytoplankton and epipelon samples for chlorophyll *a* analysis were collected weekly. Phytoplankton was sampled by filtering 1 L of pond water onto Whatman® GF/F filters. Epipelon was sampled by pooling three surface samples collected with plastic Petri dishes (4.7 cm diameter × 0.5 cm depth; Vinebrooke and Leavitt 1998). Phytoplankton and epipelon samples were stored in the dark at -20 °C until further analysis.

At the beginning, middle and end of each time treatment, grab water samples were collected in pre-rinsed 500ml polyethylene bottles. Half of the water was filtered in the field through Whatman® GF/F filters. The filtrate was analyzed for ammonium, nitrite+nitrate and dissolved organic carbon (DOC) at the University of Alberta's Water Laboratory within two days of collection. Ammonium and nitrite+nitrate were determined colorimetrically with the Technicon™ Autoanalyzer™ II using automated berthelot and cadmium reduction reactions, respectively. Total phosphorus (Prepas and Rigler 1982) and silica (Stainton et al. 1977) were determined on unfiltered samples colorimetrically with a Perkin Elmer 3300 Atomic Absorption Spectrometer. DOC was measured on an Ionic Model 1505 Programmable Carbon Analyzer (APHA (American Public Health Association) 1992) and pH was measured with a Fisher Scientific Accumet pH meter 925.

At the end of each incubation period, I placed a plastic beaker over each NDS, enclosing it and the surrounding water. The surrounding water and any dislodged organisms were preserved with a formalin-sucrose (4%) solution for invertebrate identification and

enumeration. NDS were scraped clean of algae with a soft-bristled toothbrush and rinsed with 50 ml of filtered pond water. After vigorous stirring, the samples were subdivided into one 10 ml sample preserved with Lugol's solution for microscopic examination and two 20 ml samples filtered onto Whatman® GF/F filters for chlorophyll *a* and pigment analysis. Filters were stored in the dark at -20 °C until further analysis. One rock in each pond was sampled as above to characterize the natural epilithic algal community.

Chlorophyll *a* (chl *a*) samples were extracted in 10 ml of 90% ethanol for 5 minutes at 80°C and 24 h at 4°C in the dark. Chl *a* concentration was determined fluorometrically (Shimadzu Model RF-1501, Mandel Scientific, Guelph, Ontario) following the method of Welschmeyer (1994).

Pigment samples were freeze-dried for 24 h then extracted in a 10 ml mixture of acetone, methanol and water (80:15:5 by volume) for 24 h at 10°C in the dark. Extracts were filtered (0.22 μm Acropore Nylon membrane), dried under nitrogen gas and stored in the dark at –30°C under nitrogen gas until analysis. Dried extracts were dissolved in a known volume of injection solvent of acetone, ion pairing reagent and methanol (70:25:5 by volume) containing 3.2 mg l^{-1} of the internal standard Sudan II. Pigments were separated by high performance liquid chromatography (HPLC) using a Hewlett Packard® Model 1100 with a Rainin Model 200 C18 column (Vinebrooke et al. 2002).

Epilithic algal abundance and composition were inferred from abundances of taxonomically diagnostic chlorophylls and carotenoids (Jeffrey et al. 1997). Overall abundance was inferred using Chl *a* concentration. Major algal groups identified with HPLC included chlorophytes (chl *b*); chromophytes (fucoxanthin and chl *c*), including diatoms (diatoxanthin); and Cyanobacteria (echinenone and canthaxanthin), including colonial (myxoxanthophyll) forms. Light microscopy was used to verify the proportional contribution of each taxonomic group inferred from pigment concentrations and to identify the most common algal taxa.

In addition to counting snails and caddisflies during each incubation period, total invertebrate biomass (snails, caddisflies, chironomid larvae and cladocerans) was estimated at the end of each incubation period to ensure that all grazers, including small invertebrates such as chironomid larvae and cladocerans were reduced in density and biomass on the suspended NDS (Cattaneo and Kalff 1986). All invertebrates were identified and enumerated under a dissecting microscope. Individual organisms were dried at 55°C for 24 h in pre-weighed aluminum foil drying boats, cooled in a desiccator for 24 h, then weighed on a Cahn C-31 Electrobalance to the nearest 1 μg. For snails, shell-free dry weights were determined after dissection.

Statistical Analyses

Two-tailed, *t*-tests were used to compare epilithon abundance and community structure on rocks to those on control (no nutrient enrichment, ambient grazing) NDS and to compare physical and chemical conditions in early summer to mid-summer. Univariate linear regression was used to determine whether there was any functional relationship between invertebrate density and epilithon abundance on NDS. Three-factor analyses of variance (ANOVA) were used to test for the main effects of nutrients (N), grazing (G) and time (T) and all possible interactive effects (N × G, N × T, G × T and N × G × T) on total, chlorophyte, Cyanobacteria and chromophyte abundances. Multiple comparisons among means were conducted *a posteriori* with Tukey's test (Day and Quinn 1989). Multivariate analysis of variance (MANOVA) was used to test for main and interactive effects on the relative proportions of chlorophyte (chl *b*), Cyanobacteria (canthaxanthin) and chromophyte (chl *c*). Significant treatment effects were further investigated with 3-factor ANOVAs on the relative proportions of individual chlorophylls and carotenoid. All analyses were performed on $\log_{10}(x+1)$-transformed data to approximate normal distribution before statistical analysis using JMP (SAS Institute 1996). Statistical significance was set at $\alpha = 0.05$ but weak effects ($0.05 < \alpha < 0.10$) are discussed.

RESULTS

Background physical, chemical and biological conditions

Water temperature, conductivity and pH increased and DIN (sum of ammonium, nitrite and nitrate) decreased from early to mid-summer (Table 4.1). Silica, TP and DIN:TP ratios were similar in early and mid-summer. Although NDS were closer to the water surface in mid-summer because of decreased water levels, the percentage of downwelling UV radiation reaching the NDS was similar in early and mid-summer (Table 4.1). Natural phytoplankton and epipelon abundances were similar in early and mid-summer and natural epilithon abundance increased from early to mid-summer.

Algal communities on rocks versus control NDS

Comparison of algal abundance and composition on rocks and control NDS showed that NDS had lower abundance (0.44 ± 0.19 µg cm^{-2}) than rocks (0.94 ± 0.30 µg cm^{-2}) due to fewer Cyanobacteria (*P*canthaxanthin < 0.001; *P*echinenone < 0.001) (Figure 4.2). Natural epilithic algal communities were dominated by Cyanobacteria (main taxa: *Anabaena* spp., *Gloeotrichia* sp.), whereas those on control NDS were dominated by chlorophytes (main taxa: *Bulbochaete* sp., *Mougeotia* sp.) and/or chromophytes (main taxa: *Achnanthes minutissima* Kutzing, *Cymbella* spp., *Fragilaria* spp., *Navicula* spp., *Tabellaria* spp. and small Chrysophyceae).

Effectiveness of suspending NDS in reducing grazing

During the experiment, caddisflies (*Asynarchus curtus*) and snails (*Stagnicola* sp.) were completely excluded from suspended NDS (Figure 4.3a). Caddisfly and snail densities on the bottom NDS decreased in mid-summer (Table 4.2). Exclusion of caddisflies and snails on suspended NDS did not result in an increase in chironomid larvae (*Cladotanytarsus* sp., *Procladius* sp.) and cladocerans (*Chydorus sphaericus, Alona gutata, Daphnia rosea*) (Table 4.2; Figure 4.3b). Therefore, suspending NDS successfully produced a reduced grazer treatment by excluding caddisflies and snails, and consequentially decreasing total invertebrate biomass.

Table 4.1: Mean (standard error, n = 3) physical and chemical conditions during early and mid-summer in three alpine ponds. DIN is the sum of ammonia, nitrite and nitrate; TP is total phosphorus; and DOC is dissolved organic carbon. Significant differences between early and mid-summer are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.001$).

	Early summer	**Mid-summer**
Mean daily water temperature (°C)	***10.3 (0.3)	13.2 (0.3)
Conductivity (μS cm^{-1})	***51.9 (9.9)	91.3 (8.3)
pH	**6.9 (0.5)	7.7 (0.8)
Silica (mg l^{-1})	0.84 (0.21)	0.62 (0.28)
DIN (µg l^{-1})	*29.1 (5.2)	15.15 (5.5)
TP (µg l^{-1})	33.1 (3.3)	27.4 (3.52)
DIN:TP[1]	0.90 (0.19)	0.63 (0.20)
NDS depth below surface (cm)	***10.5 (0.3)	6.5 (0.2)
DOC (mg l^{-1})	6.47 (0.60)	6.42 (0.65)
% UVB on NDS[2]	29.4 (3.6)	28.5 (4.0)
% UVA on NDS[2]	69.0 (8.8)	66.8 (9.7)
Phytoplankton abundance Chl *a* (µg l^{-1})	2.58 (0.34)	2.08 (0.37)
Epipelon abundance Chl *a* (µg cm^{-2})	7.66 (3.10)	10.11 (3.27)
Epilithon abundance Chl *a* (µg cm^{-2})	* 0.49 (0.32)	1.39 (0.32)

1. DIN:TP was found as the best index of nutrient limitation for alpine lake phytoplankton, DIN:TP < 1 suggests N-limitation (Morris and Lewis 1988).
2. Percentage of downwelling UVB and UVA reaching the NDS were estimated based on DOC using equations from temperate lakes (Scully and Lean 1994). Although these equations likely underestimate downwelling UVA and UVB in alpine ponds, they should provide useful values for temporal comparison.

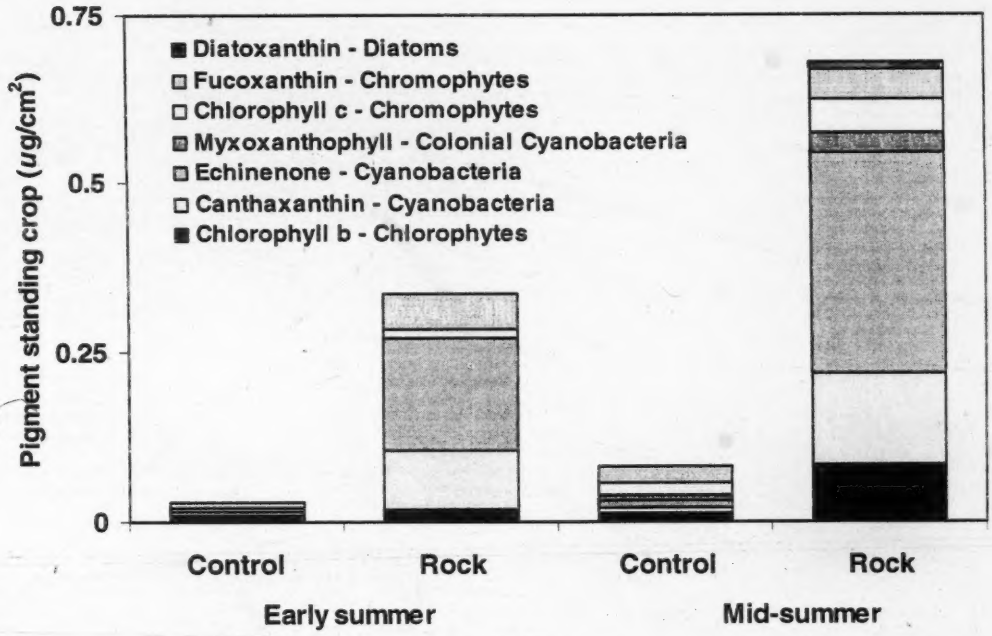


Figure 4.2: Mean (n = 3) algal abundance and community composition inferred from taxonomically diagnostic chlorophylls and carotenoids on control NDS and rocks in early and mid-summer from three alpine ponds.

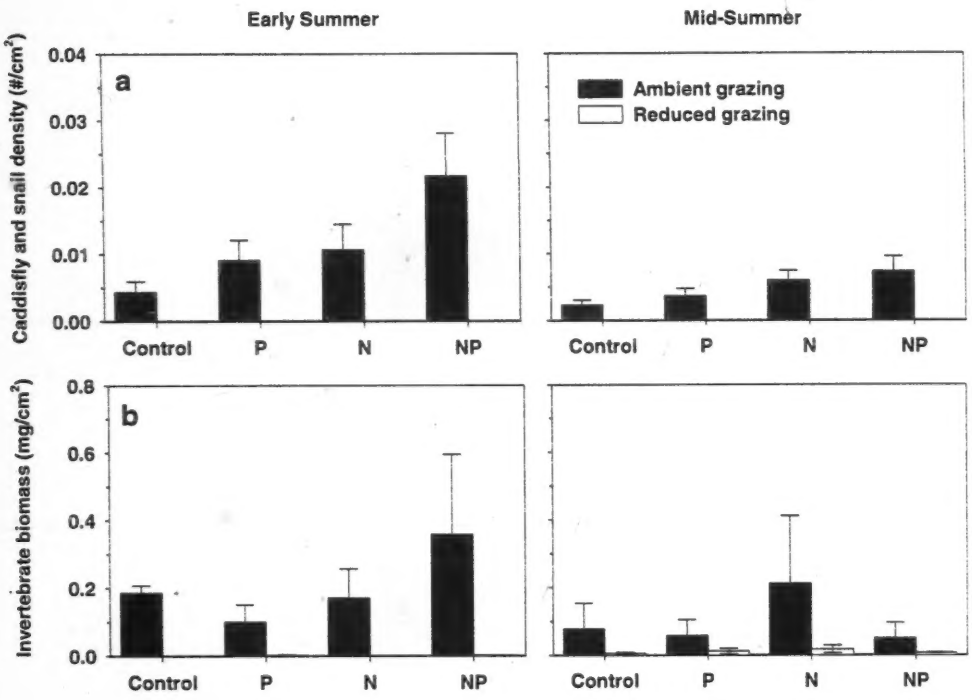


Figure 4.3: Caddisfly and snail density (mean ± SE, n = 3) on NDS during the experiment (a) and total invertebrate (caddisfly, snail, chironomid larva and cladocerans) biomass (mean ± SE, n = 3) at the end of the experiment (b). Results are given for experiments conducted in early and mid-summer for each nutrient treatment (Control, no nutrient enrichment; P, phosphorus enrichment; N, nitrogen enrichment; and NP, nitrogen and phosphorus enrichment) and for each grazer treatment (solid bars, ambient grazing and white bars, reduced grazing treatment).

Table 4.2: Three-factor ANOVA treatment effects on caddisfly and snail density during the experiment and total invertebrate biomass at the end of the experiment. Nutrient effects refer to control, P enrichment, N enrichment and P+N enrichment treatments. Significant contrasts among means were conducted *a posteriori* with the Tukey's test to determine significant differences between nutrient enrichment treatments. Grazer effects refer to reduced and ambient grazing treatments and season effects refer to the early summer and mid-summer treatments. Reported are degrees of freedom, F statistics and p-values for $n = 3$ replicates. Effects at $P < 0.05$ are printed in bold and trends at $0.05 < P < 0.1$ are printed in italic.

		Caddisfly and snail density (during)		Total invertebrate biomass (end)	
Effects	df	*F*	p	*F*	p
Nutrient	3	**7.11**	**<0.001**	0.41	0.748
Contrasts			**NP > C**		
Grazer	1	**86.38**	**<0.001**	**14.23**	**<0.001**
Time	1	**14.36**	**<0.001**	1.49	0.231
N×G	3	**7.11**	**<0.001**	0.40	0.755
N×T	3	*2.31*	*0.076*	0.71	0.555
G ×T	1	**14.36**	**<0.001**	2.23	0.145
N×G×T	3	*2.31*	*0.076*	0.60	0.619

Treatment effects on epilithic algae abundance

Total epilithon abundance (chl *a*) increased significantly with NP enrichment (Table 4.3) and abundance generally increased from control and P to N to NP NDS suggesting N-limitation (Figure 4.4). While in general, grazing slightly reduced epilithic algal abundance, grazing pressure was not sufficient to mask increased algal abundance due to nutrient enrichment (no nutrient-grazer interaction; Table 4.3; Figure 4.4). Total epilithon abundance increased most when nutrient addition and grazer removal were combined (Figure 4.4). Epilithic algal abundance inferred from chl *a* measured fluorometrically was higher in mid-summer than early summer but neither nutrient nor grazer effects on total epilithon abundance were time-dependent (Table 4.3).

Treatment effects on epilithic community composition

Each algal group responded slightly different to nutrient enrichment. Chlorophyte abundance increased significantly with NP enrichment in both early and mid-summer (Table 4.4) and abundance generally increased from control and P to N to NP NDS (Figure 4.5). Cyanobacteria abundance (canthaxanthin and echinenone) increased with P enrichment relative to N enrichment (Table 4.4; Figure 4.6a-b), whereas colonial Cyanobacteria abundance (myxoxanthophyll) increased significantly with NP enrichment (Table 4.4; Figure 4.6c). Nutrient effects on Cyanobacteria abundance inferred from echinenone and myxoxanthophyll were only significant in mid-summer (Table 4.4; Figure 4.6). Chromophyte abundance (chl *c*) increased weakly with NP enrichment in both early and mid-summer (Table 4.4; Figure 4.7a) and diatom abundance (diatoxanthin) was not significantly affected by nutrient enrichment but abundance was generally highest on the N NDS (Figure 4.7c).

Grazing had no effect on abundances of chlorophyte and Cyanobacteria (Table 4.4), but caused a decrease in chromophyte abundance (chl *c*) in both early and mid-summer (Table 4.4; Figures 5-7c). Overall, nutrient effects on community composition did not depend on grazing pressure (no nutrient-grazer interactions; Table 4.4). However, chlorophyte abundance increased significantly when NP enrichment and grazing were

Table 4.3: Three-factor ANOVA treatment effects on epilithon abundance inferred from chlorophyll *a* measured on the fluorometer and HPLC. Details as in Table 4.2.

		Chlorophyll *a* (Fluorometer)		Chlorophyll *a* (HLPC)	
Effects	df	***F***	p	***F***	p
Nutrient	3	**7.70**	**<0.001**	**7.65**	**<0.001**
Contrasts			NP > C		NP > C
Grazer	1	*2.96*	*0.095*	*2.96*	*0.095*
Time	1	**6.22**	**0.018**	0.00	0.957
N×G	3	0.37	0.776	0.44	0.723
N×T	3	0.24	0.871	0.15	0.929
G ×T	1	0.08	0.773	0.44	0.512
N×G×T	3	0.07	0.977	0.84	0.481

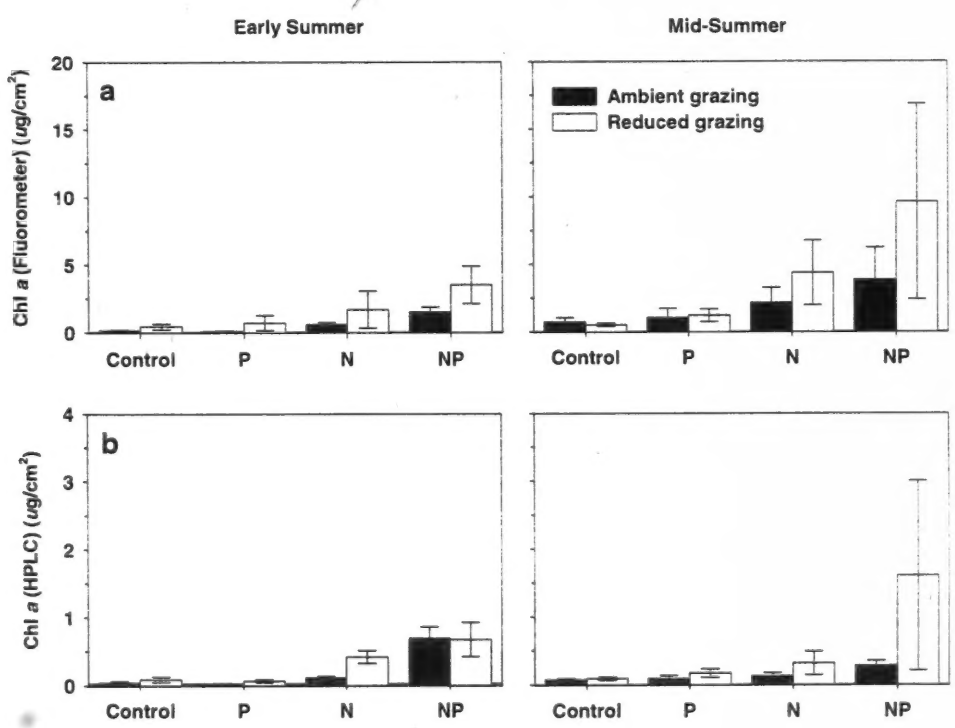


Figure 4.4: Epilithon abundance (mean ± SE, n = 3) inferred from chlorophyll *a* measured by fluorometer (a) and HPLC (b) from NDS experiments in early and mid-summer. Treatments and symbols as in Figure 4.3.

Table 4.4: Three-factor ANOVA treatment effects on epilithon chlorophyte abundance inferred from chlorophyll *b;* Cyanobacteria abundance inferred from canthaxanthin, echinenone and myxoxanthophyll; and chromophyte abundance inferred from chlorophyll *c*, fucoxanthin and diatoxanthin. Details as in Table 4.2.

		Chlorophyte		Cyanobacteria						Chromophyte					
		Chlorophyll *b*		Canthaxanthin		Echinenone		Myxoxanthophyll		Chlorophyll *c*		Fucoxanthin		Diatoxanthin	
Effects	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Nutrient	3	**3.59**	**0.024**	**4.61**	**0.009**	**4.06**	**0.015**	**3.66**	**0.035**	*2.58*	*0.071*	1.47	0.242	1.34	0.278
Contrasts			**NP > C**		**P > N**		**P > N**		**NP > P**						
Grazer	1	0.17	0.682	2.39	0.132	2.16	0.152	0.22	0.643	**5.23**	**0.029**	2.15	0.152	1.75	0.195
Time	1	1.71	0.201	**13.69**	**<0.001**	**8.50**	**0.006**	**29.46**	**<0.001**	0.27	0.610	*2.95*	*0.096*	**7.06**	**0.012**
N×G	3	0.14	0.938	0.86	0.469	0.21	0.887	0.74	0.543	0.72	0.547	0.53	0.664	0.34	0.800
N×T	3	0.62	0.609	1.83	0.161	**3.84**	**0.019**	**4.01**	**0.026**	0.12	0.947	0.35	0.792	0.32	0.813
G ×T	1	1.97	0.170	0.23	0.633	0.36	0.554	0.47	0.501	0.71	0.404	0.07	0.800	0.12	0.733
N×G×T	3	1.14	0.346	1.06	0.380	0.74	0.536	0.75	0.539	0.65	0.590	0.26	0.852	0.08	0.970

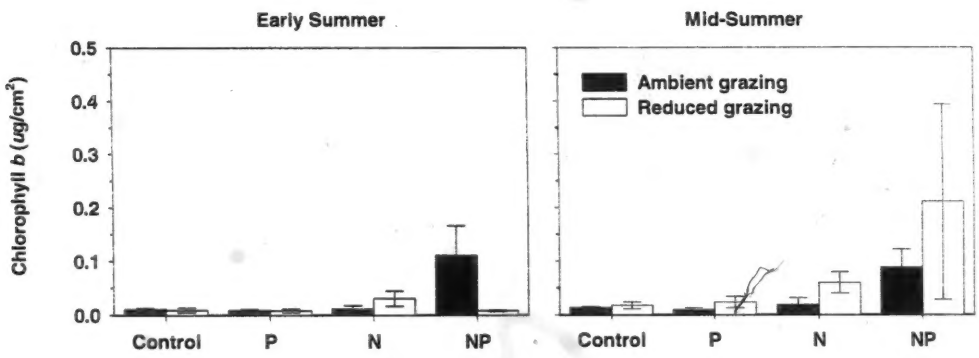


Figure 4.5: Epilithon chlorophyte abundance (mean ± SE, n = 3) inferred from chlorophyll *b* in early and mid-summer. Treatments and symbols as in Figure 4.3.

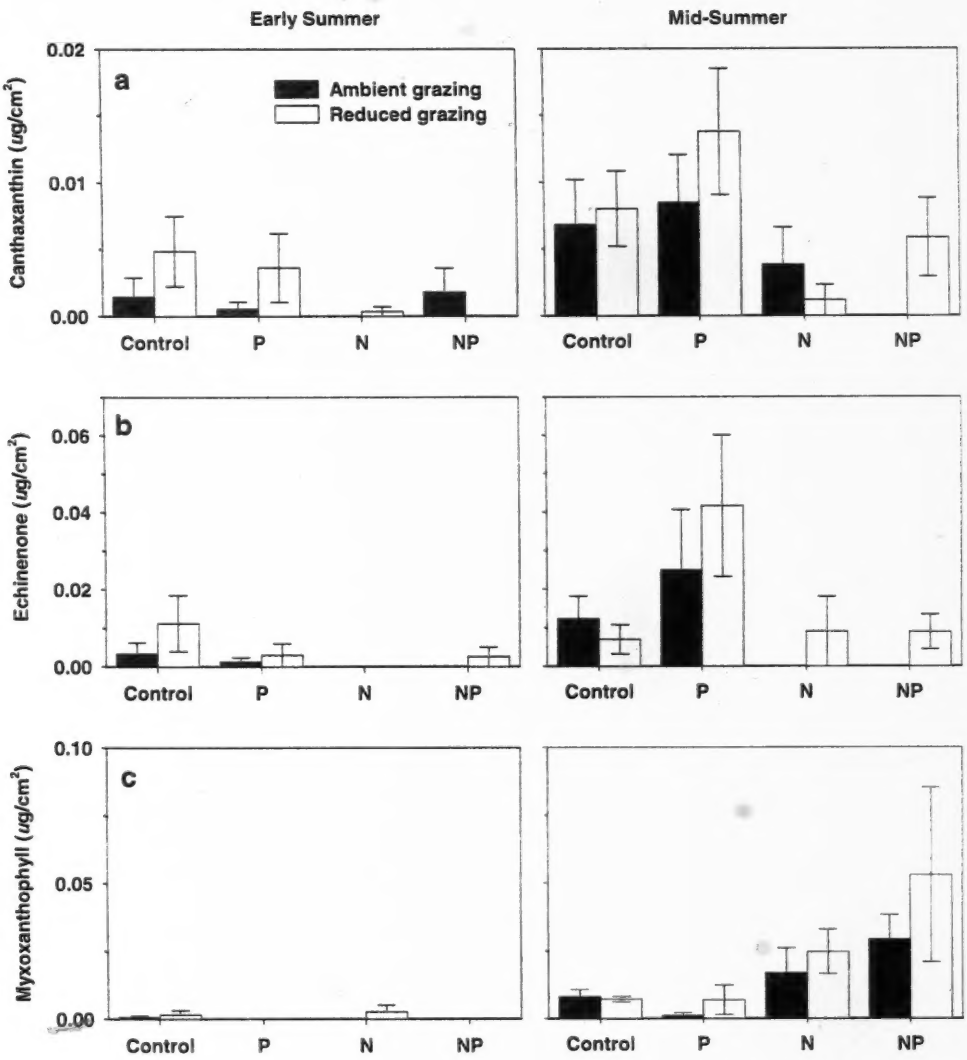


Figure 4.6: Epilithon Cyanobacteria abundance (mean ± SE, n = 3) inferred from canthaxanthin (a), echinenone (b) and myxoxanthophyll (c) in early and mid-summer. Treatments and symbols as in Figure 4.3.

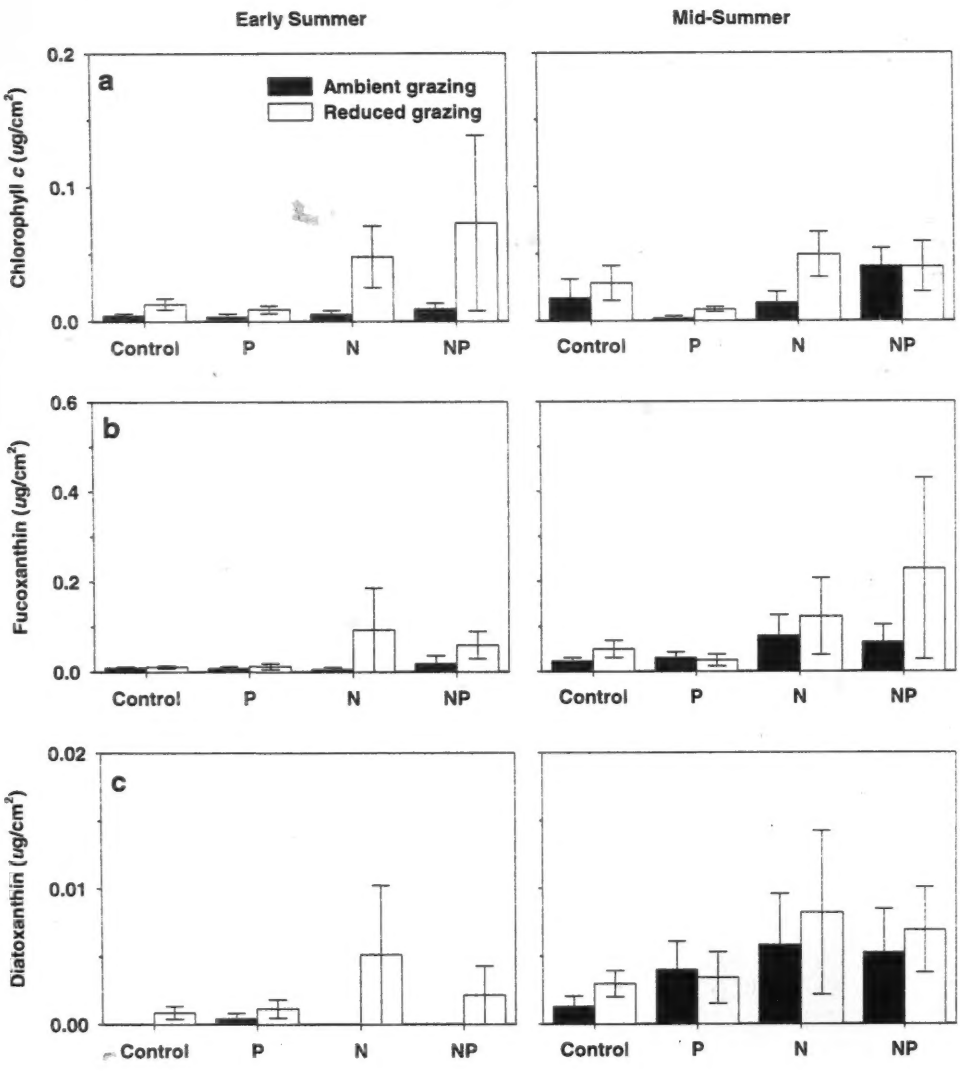


Figure 4.7: Epilithon chromophyte abundance (mean ± SE, n = 3) inferred from chlorophyll *c* (a), fucoxanthin (b) and diatoxanthin (c) in early and mid-summer. Treatments as in Figure 4.3.

combined in early summer (Figure 4.4). Similarly, Cyanobacteria abundance (canthaxanthin) increased weakly when NP enrichment and grazing were combined in early summer and when N enrichment and grazing were combined in mid-summer (Figure 4.6a).

The relative proportions of epilithic algal groups varied among treatments (Table 4.5). The relative proportion of Cyanobacteria (canthaxanthin) increased with P enrichment relative to NP enrichment (Table 4.5; Figure 4.8). The relative proportion of Cyanobacteria also increased in mid-summer (Table 4.5). The relative proportion of chromophyte (chl *c*) decreased with grazing, but this grazing effect was only significant in early summer (grazer-time interaction; Table 4.5).

Nutrient effects on grazer abundance

Changes in algal biomass and composition among nutrient treatments affected grazer abundance. During the experiment, caddisfly and snail density increased significantly on ambient NDS with NP enrichment (Table 4.2). Densities generally increased from control to P to N to NP NDS (Figure 4.8). This resulted in a positive relationship between epilithon abundance and caddisfly and snail density ($r^2 = 0.36$; $P < 0.001$). However, total invertebrate biomass at the end of the experiment was unaffected by nutrient enrichment (Table 4.2).

DISCUSSION

Epilithic algae in these western Canadian alpine ponds are N-limited. When NDS enriched with nutrients were installed in alpine ponds, abundance of the total community (expressed as Chl *a*) increased in response to added N and NP. N-limited algal growth has been documented in subalpine and alpine lakes throughout the western United States (Morris and Lewis 1988; Goldman et al. 1993; Axler and Reuter 1996; Interlandi et al. 1999; Sickman 2001; Lafrançois 2002). Although algal community abundance increased in response to N addition, not all algal taxa responded similarly. Cyanobacteria (inferred from abundances of canthaxanthin, echinenone) although not always dominating, reached their highest proportions on P enriched substrates. Chlorophytes and chromophytes

Table 4.5: Three-factor MANOVA and ANOVA treatment effects on epilithon community composition as proportions of chlorophyll *b* (chlorophyte), canthaxanthin (Cyanobacteria) and chlorophyll *c* (chromophyte). For the MANOVA the Pillai Trace *F* statistic is given. Details as in Table 4.2.

		MANOVA		Chlorophyll *b*		Canthaxanthin		Chlorophyll *c*	
Effects	df			*F*	p	*F*	p	*F*	p
Nutrient	3	**2.27**	**0.024**	0.66	0.578	**3.28**	**0.033**	1.41	0.258
Contrasts							P > NP		
Grazer	1	1.34	0.281	2.28	0.141	0.45	0.506	**15.11**	**<0.001**
Time	1	**5.96**	**0.003**	0.01	0.946	**6.66**	**0.015**	1.07	0.310
N×G	3	0.55	0.820	0.73	0.539	0.65	0.591	0.11	0.955
N×T	3	1.40	0.200	0.57	0.638	1.24	0.313	0.71	0.552
G ×T	1	1.50	0.236	2.79	0.104	2.31	0.138	**4.39**	**0.042**
N×G×T	3	0.70	0.714	0.07	0.976	0.63	0.604	1.13	0.350

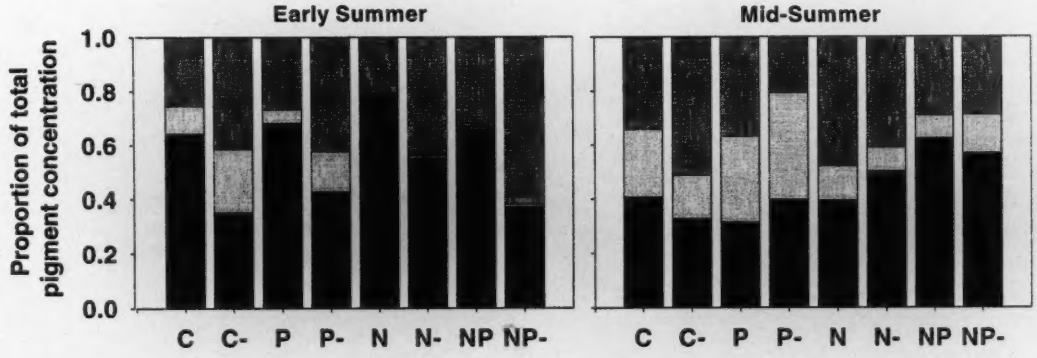


Figure 4.8: Proportional contribution of each algal group to total pigment concentration at the end of NDS experiments in early (left) and mid-summer (right). Algal groups are chlorophyte (chlorophyll *b* - black), Cyanobacteria (canthaxanthin – light gray) and chromophyte (chlorophyll *c* – dark gray). The treatments are abbreviated as C (control), P (phosphorus), N (nitrogen) and NP (nitrogen and phosphorus). The minus sign denotes reduced grazing treatment.

dominated singly or collectively on N and NP enriched substrates. Chlorophytes were primarily N-limited but became P-limited after N-enrichment - they increased further with NP enrichment. Chromophytes were primarily N-limited - they did not increase further with NP enrichment. Others have also observed shifts in community composition of algae because of nutrient enrichment (Fairchild et al. 1985; Peterson and Grimm 1992; Rosemond et al. 1993; Lafrançois 2002). Cyanobacteria dominance is a common occurrence in phytoplankton communities after P enrichment to N:P ratios below Redfield ratios (Schindler 1977; Smith and Bennett 1999). However, in benthic algal communities, P enrichment has led to Cyanobacteria dominance in some (Fairchild et al. 1985) but not all experiments (Rosemond et al. 1993; Lafrançois 2002). Chlorophyte and/or chromophyte dominance after N enrichment to N:P ratios above Redfield ratios were found in both planktonic (Schindler 1977) and benthic algal communities (Fairchild et al. 1985; Peterson and Grimm 1992; Rosemond et al. 1993). The community composition of epilithic algae in alpine ponds should shift from Cyanobacteria dominance to chlorophyte and chromophyte dominance or even diatom dominance after anthropogenic N enrichment.

In these alpine ponds, N limitation by the epilithic algae community was associated with low water column N:P ratios. N-limitation has also been linked to low water column N:P ratios in other subalpine and alpine lakes (DIN:TP $\leq$ 1) (Morris and Lewis 1988; Sickman 2001; Lafrançois 2002). Low N:P ratios in alpine ponds are likely maintained by both external and internal mechanisms, similar to other aquatic systems (Vitousek and Howarth 1991). Nutrient inputs to alpine aquatic systems tend to have low N:P ratios because the terrestrial vegetation in their watersheds is typically N-limited (Bowman et al. 1993; Campbell et al. 2000). The fact that N-fixing Cyanobacteria (*Anabaena* sp., *Gloeotrichia* sp.) dominate the natural epilithon communities in these alpine ponds suggests N-fixation is an essential N source. Yet N-fixation is probably inhibited in alpine ponds by cold and variable water temperatures, oxygen saturation (Howarth et al. 1988) and high ultraviolet radiation (Higley et al. 2001). Lastly, low N:P ratios are likely maintained by bacteria that retain N and release P in this low N:P environment (Tezuka 1989).

Herbivory generally decreased epilithic abundance in alpine ponds, agreeing with observations in lakes and streams (Feminella and Hawkins 1995; Steinman 1996). Herbivores are abundant in alpine ponds because vertebrate predators are absent and most invertebrate predators are reduced or eliminated every winter when the ponds freeze solid. Increased algal densities on NDS enriched with nutrients appeared to alleviate food limitation, as evident by the positive correlation between invertebrate densities and algal abundance. Although food quality was not determined in this study, invertebrates were probably limited by both food quantity and quality (Hillebrand and Kahlert 2001; Frost and Elser 2002).

Although invertebrates responded to increases in algal abundace, not all algal groups were equally grazed. Chlorophyte abundance generally decreased with grazing. However, in early summer, proliferation of a grazer-resistant species, gelatinous *Tetraspora* sp., on NP enriched substrate allowed chlorophytes to take advantage of nutrient enriched conditions without competition from other grazer-susceptible species. Cyanobacteria abundance was also not always reduced with grazing because of the presence of grazer-resistant species, firmly-attached gelatinous *Nostochopsis* sp. and *Gloeotrichia* sp. Diatom abundance was consistently reduced with grazing, supporting other studies that have found diatoms dominate in low grazer environments and decrease significantly with grazing (Cuker 1983; Lowe and Hunter 1988; Power et al. 1988; Marks and Lowe 1989; Rosemond et al. 1993). In this study, diatoms were likely susceptible to grazing because there were few grazer-resistant morphologies and there were many loosely attached taxa that were susceptible to dislodgement during non-consumptive grazer activities. Therefore, decreases in epilithic algal abundance may be linked primarily to the loss of diatoms rather than chlorophytes and Cyanobacteria.

Both nutrient enrichment and invertebrate grazing were important controls of epilithic algal abundance and community structure in alpine ponds. However, nutrient enrichment generally had a greater effect than invertebrate grazing on epilithon abundance. As a result, grazers were unable to mask the overall response of the algal community to

enrichment, despite the fact that grazers were abundant and food limited. There are several possible reasons for the inability of grazers to mask the nutrient response. One possible explanation is that the dominant algal species responding to nutrient enrichment were grazer resistant, gelatinous *Tetraspora* sp. and *Nostochopsis* sp. However, this is inconsistent with the idea that increased grazer resistance is accompanied by reduced competitive ability (Rosemond et al. 1993). Another possible explanation is that the experiment was too short (33 days) and that in a longer experiment, grazer density may increase, resulting in a greater grazer control. For example, in a tundra river fertilization experiment, algal abundance increased in the first two years, after which grazer density and biomass increased damping the algal response to nutrient enrichment (Peterson et al. 1993). However, similar to previous studies (Rosemond et al. 2000, Hillebrand and Kahlert 2001), invertebrate grazing did have a greater effect than nutrient enrichment on diatom abundance in these ponds. As a result, grazers masked the diatom response to nutrient enrichment. Thus nutrient enrichment had a greater effect than invertebrate grazing on total algal, chlorophyte and Cyanobacteria abundance and invertebrate grazing had greater effect than nutrient enrichment on diatom abundance.

Higher overall epilithon and Cyanobacteria abundance in mid-summer than in early summer can be explained by both manipulated and non-manipulated factors. In mid-summer, as caddisflies emerged, the grazer control weakened, allowing algal abundance to increase. Water temperature also increased in mid-summer leading to typical increases in algal abundance and pigment accrual (DeNicola 1996; Baulch 2001). A similar increase in benthic algal abundance from early to late summer has been found in arctic ponds as water temperatures increased (Sheath and Hellebust 1978; Alexander et al. 1980). The increase in Cyanobacteria abundance in mid-summer was probably due to both warmer water temperatures (DeNicola 1996) and lower ambient N concentrations and N:P ratios. In contrast, the increase in chromophyte abundance in mid-summer was not expected. I initially expected chromophyte abundance to decrease in mid-summer as water temperatures increased (DeNicola 1996). However, given that chromophytes were particularly vulnerable to grazing, chromophytes likely increased in mid-summer due to

declining grazer densities. The relative importance of nutrient availability and herbivory in controlling total epilithic algal abundance did not change seasonally.

One limitation of this study was that algal abundance and community composition on control NDS did not mimic that on natural rocks. NDS likely underestimated total epilithon abundance found on natural rocks due to differences in the amount of sediment and stage of community succession. NDS were covered in less sediment than natural rocks and therefore had less epipelic algae. Considering epipelon abundance was two to 64 times greater than epilithon abundance in a given area (Table 4.1), even a small decrease in the amount of sediment could result in a large decrease in total algal abundance. Epilithon communities on NDS were at an earlier successional stage than communities on rocks and consistent with previous work (Hoagland et al. 1982; Peterson and Grimm 1992) had lower total epilithon and Cyanobacteria abundance than natural rocks. Despite underestimating total epilithon and Cyanobacteria abundance, the use of NDS allowed experimentation on the early successional epilithic algal community, which is particularly relevant in alpine ponds because algal communities are continually disturbed by wind, desiccation and freezing.

In conclusion, these results indicate that initial responses of alpine ponds to increased N deposition are likely to be increased algal abundance and a shift in community structure to chlorophyte and chromophyte dominance or even diatom dominance. Initially grazer biomass increases in response to the greater food supply. In turn, it dampens some of the original algal response to nutrient enrichment. N loading to alpine aquatic systems is expected to increase due to increased direct atmospheric N deposition (Vitousek et al. 1997) and modification of the terrestrial N budget (Williams et al. 1996b; Hobbie and Chapin 1998). Persistent N deposition could cause a shift in nutrient status from N- to P-limitation. For example, atmospheric N deposition is implicated in the shift from NP- to P-limitation in Lake Tahoe (Goldman et al. 1993; Jassby et al. 1994) and the shift in diatom composition in Colorado Front Range lakes (Baron et al. 2000; Wolfe et al. 2001). These predicted changes in nutrient status of alpine ponds do not consider other anthropogenic stressors, such as altered temperature and precipitation regimes,

acidification, UV radiation and accumulation of toxicants that may also impact alpine pond nutrient budgets and algal and invertebrate communities (Schindler 1997; Schindler 2001). However, these results indicate that even in the absence of other anthropogenic stressors, increased N loading may significantly modify alpine pond ecosystems.

REFERENCES

Alberta Environment. 2003. Unpublished database. Evaluation and Reporting Section. Environmental Monitoring and Evaluation Branch. 9820 - 106 Street, Edmonton, Alberta, Canada.

Alexander, V., Stanley, D.W., Daley, R.J. and McRoy, C.P. 1980 Primary Producers. *In* Limnology of Tundra Pond *Edited by* J.E. Hobbie. Dowden, Hutchinson and Ross, Inc., Pennsylvania, United States. pp. 179-250.

APHA (American Public Health Association), American Water Works Association and Water Environment Federation (1992) Standard Methods for the Examination of Water and Wastewater. 18th Ed. APHA, Washington, D.C.

Axler, R.P. and Reuter, J.E. 1996. Nitrate uptake by phytoplankton and periphyton: Whole lake enrichment and mesocosm ^{15}N experiment in an oligotrophic lake. Limnology and Oceanography **41**: 659-671.

Baron, J.A., Rueth, H.M., Wolfe, A.M., Nydick, K.R., Allstott, E.J., Minear, J.T. and Moraska, B. 2000. Ecosystem response to nitrogen deposition in the Colorado Front Range. Ecosystems **3**: 352-368.

Baulch, H.M. 2001. Effects of increased temperature on epilithon and the implications of climate change. M.Sc. thesis, University of Alberta, Edmonton, Alberta, Canada.

Beder, K. 1967 Ecology of the alpine vegetation of Snow Creek Valley, Banff National Park, Alberta. M.Sc. thesis, University of Calgary, Calgary, Alberta, Canada.

Bowman, W.D., Theodose, T.A., Schardt, J.C. and Conant, R.T. 1993. Constraints of nutrient availability of primary production in two alpine tundra communities. Ecology **74**: 2085-2097.

Brett, M.T. and Goldman, C.R. 1997. Consumer versus resource control in freshwater pelagic food webs. Science **275:** 384-386.

Campbell, D.H., Baron, J.A., Tonnessen, K.A., Brooks, P.S. and Schuster, P.F. 2000. Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resources Research **36**: 37-47.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, X.H.E. and von Ende, C.N. 1987. Regulation of lake primary productivity by food web structure in whole-lake experiments. Ecology **68**: 1863-1876.

Cattaneo, A. and Kalff, J. 1986. The effect of grazer size manipulation on periphyton communities. Oecologia **69:** 612-617.

Cuker, B.E. 1983. Grazing and nutrient interactions in controlling the activity and composition of the epilithic algal community of an arctic lake. Limnology and Oceanography **28:** 133-141

Day, R.W. and Quinn, G.P. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs **59**: 433-463

DeNicola, D.M. 1996. Periphyton responses to temperature at different ecological levels. *In* An introduction to algal ecology in freshwater benthic habitats. *Edited by* R.J. Stevenson, M.L. Bothwell and R.L. Lowe. Academic Press, Toronto. pp. 150-183.

Fairchild, G.W., Lowe, R.L. and Richardson, W.B. 1985. Algal periphyton growth on nutrient-diffusing substrates: an *in situ* bioassay. Ecology **66:** 465-472.

Feminella, J.W. and Hawkins, C.P. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. Journal of North American Benthological Society **14:** 465-509.

Frost, P.C. and Elser, J.J. 2002. Effects of light and nutrients on the net accumulation and elemental composition of epilithon in boreal lakes. Freshwater Biology **47:** 173-183.

Goldman, C.R., Jassby, A.D. and Hackley, S.H. 1993. Decadal, interannual and seasonal variability in enrichment bioassays at Lake Tahoe, California-Nevada, USA. Canadian Journal of Fisheries and Aquatic Sciences **50:** 1489-1496.

Higley, B., Carrick H.I., Brett, M.T., Luecke, C. and Goldman, C.R. 2001. The effects of ultraviolet radiation and nutrient additions on periphyton abundance and composition

in a sub-alpine lake (Castle Lake, USA). International Review of Hydrobiology **86:** 147-163.

Hillebrand, H. and Kahlert, M. 2001. Effect of grazing and nutrient supply on periphyton abundance and nutrient stoichiometry in habitats of different productivity. Limnology and Oceanography **46:** 1881-1898.

Hoagland, K.D., Roemer, S.D. and Rosowski, J.R. 1982. Colonization and community structure of two periphyton assemblages, with emphasis on the diatoms (Bacillariophyceae). American Journal of Botany **69:** 188-213.

Hoagland, K.D., Zlotsky, A. and Peterson, C.G. 1986 The source of algal colonizers on rock substrates in a freshwater impoundment. *In* Algal biofouling *Edited by* L.V. Evans and K.D. Hoagland. Elsevier Science Publishers, Amsterdam, Netherlands. pp. 21-39.

Hobbie, S.E. and Chapin III, F.S. 1998. The response of tundra plant abundance, aboveground production, nitrogen and CO_2 flux to experimental warming. Ecology **79:** 1526-1544.

Holland, W.D. and Coen, G.M., Editors. 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume II: Soil and Vegetation Resources and Map Supplement. Alberta Institute of Pedology.

Howarth, R.W., Marino, R. and Cole, J.J. 1988. Nitrogen fixation in freshwater, estuarine and marine ecosystems: 2. Biogeochemical controls. Limnology and Oceanography **33:** 688-701.

Interlandi, S.J., Kilham, S.S. and Theriot, E.C. 1999. Response of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. Limnology and Oceanography **44:** 668-682.

Jassby, A.D., Reuter, J.E., Axler, R.P., Goldman, C.R. and Hackley, S.H. 1994. Atmospheric deposition of nitrogen and phosphorus in the annual nutrient load of Lake Tahoe (California-Nevada). Water Resources Research **30:** 2207-2216.

Jeffrey, S.W., Mantoura, R.F.C. and Wright, S.W. 1997. Phytoplankton pigments in oceanography. UNESCO Publishing, Paris.

Lafrançois, B.M. 2002. Algal and invertebrate response to atmospheric nitrogen deposition in rocky mountain lakes. PhD thesis, Colorado State University, Fort Collins, Colorado, United States.

Lamberti, G.A. and Resh, V.H. 1983. Stream periphyton and insect herbivores: An experimental study of grazing by a caddisfly population. Ecology **64:** 1124-1135.

Leibold, M.A. and Wilbur, H.M. 1992. Interactions between food-web structure and nutrients on pond organisms. Nature **360:** 341-343.

Lowe, R.L. and Hunter, R.D. 1988. Effect of grazing by *Physa integra* on periphyton community structure. Journal of North American Benthological Society **7:** 29-36.

Marks, J.C. and Lowe, R.L. 1989. The independent and interactive effects of snail grazing and nutrient enrichment on structuring periphyton communities. Hydrobiologia **185:** 9-17.

Morris, D.P. and Lewis, W.M. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biology **20:** 315-327.

Oksanen L., Fretwell, S.D., Arruda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118:** 240-261.

Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M., Moller, B., Ford, T.E., Hershey, A., Hiltner, A., Kipphut, G., Lock, M.A., Fiebig, D.M., McKinley, V., Miller, M.C., Vestal, J.R., Ventullo, R. and Volk, G. 1993. Biological responses of a tundra river to fertilization. Ecology **74:** 653-672.

Peterson, C.G. and Grimm, N.B. 1992. Temporal variation in enrichment effects during periphyton succession in a nitrogen-limited desert stream ecosystem. Journal of North American Benthological Society **11:** 20-36.

Peterson, C.G., Horton, M.A., Marshall, M.C., Valett, H.M. and Dahm, C.N. 2001. Spatial and temporal variation in the influence of grazing macroinvertebrates on epilithic algae in a montane stream. Archiv für Hydrobiologie **153:** 29-54.

Power, M.E., Stewart, A.J. and Matthews, W.J. 1988 Grazer control of algae in an Ozark Mountain stream: Effects of short-term exclusion. Ecology **69:** 1894-1898.

Prepas, E. E. and Rigler, F.H. 1982. Improvements in quantifying the phosphorus concentration in lake water. Canadian Journal of Fisheries and Aquatic Sciences **39:** 822-829.

Rosemond, A.D., Mulholland, P.J. and Brawley, S.H. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage abundance and productivity to variation in light, nutrients and herbivores. Canadian Journal of Fisheries and Aquatic Sciences **57:** 66-75.

Rosemond, A.D., Mulholland, P.J. and Elwood, W. 1993. Top-down and bottom-up control of stream periphyton: Effects on nutrients and herbivores. Ecology **74:** 1264-1280.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science **195:** 260-262.

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. Hydrological Processes **11:** 1043-1067.

Schindler, D.W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Canadian Journal of Fisheries and Aquatic Sciences **58:** 1-12.

Scrimgeour, G.J. and Chambers, P.A. 1997. Development and application of a nutrient-diffusing bioassay for large rivers. Freshwater Biology **38:** 221-231.

Scully, N.M. and Lean, D.R.S. 1994 The attenuation of ultraviolet radiation in temperate lakes. Ergebnisse der Limnologie **43:** 134-144.

Sheath, R.G. and Hellebust, J.A. 1978. Comparison of algae in the euplankton, tychoplankton and periphyton of a tundra pond. Canadian Journal of Botany **56:** 1472-1483.

Sickman, J.O. 2001. Comparative analysis of nitrogen biogeochemistry in high elevation ecosystems. Ph.D. thesis, University of California, Santa Barbara, California, United States.

Smith, V.H and Bennett, S.J. 1999. Nitrogen:phosphorus supply ratios and phytoplankton community structure. Archiv für Hydrobiologie **146:** 37-53.

Stainton, M.P., Capel, M.J. and Armstrong, F.A.J. 1977. The Chemical Analysis of Freshwater. 2nd Ed. Fisheries Environment Canada Miscellaneous Special Publication. 25: 180 pp.

Steinman, A.D. 1996. Effects of grazers on freshwater benthic algae. *In* An introduction to algal ecology in freshwater benthic habitats. *Edited by* R.J. Stevenson, M.L. Bothwell and R.L. Lowe. Academic Press, Toronto. pp. 341-374.

Tezuka, Y. 1989. The C-N-P ratio of phytoplankton determines the relative amounts of dissolved inorganic nitrogen and phosphorus release during aerobic decomposition. Hydrobiologia **173:** 55-62.

Vinebrooke, R.D., Dixit, S.S., Graham, M.D., Gunn, J.M., Chen, Y. and Belzile, N. 2002. Whole-lake algal responses to a century of acidic industrial deposition on the Canadian Shield. Canadian Journal of Fisheries and Aquatic Sciences **59:** 483-493.

Vinebrooke, R.D. and Leavitt, P.R. 1998. Direct and interactive effects of allochthonous dissolved organic matter, inorganic nutrients and ultraviolet radiation on an alpine littoral food web. Limnology and Oceanography. **43:** 1065-1081.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. and Tilman, D.G. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications **7:** 737-750.

Vitousek, P.M. and Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry **13:** 87-115.

Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography **39:** 1985-1992.

Williams, M.W., Baron, J.S., Caine, N., Sommerfeld, R. and Sanford, R. 1996a. Nitrogen saturation in the Rocky Mountains. Environmental Science and Technology **30**: 640-646.

Williams, M.W., Losleben, M., Caine, N. and Greenland, D. 1996b. Changes in climate and hydrochemical responses in a high-elevation catchment in the Rocky Mountains, USA. Limnology and Oceanography **41**: 939-946.

Wolfe, A.P., Baron, J.S. and Cornett, R.J. 2001. Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). Journal of Paleolimnology **25:** 1-7.

CHAPTER 5: GENERAL CONCLUSIONS

Alpine ponds I studied are physically demanding environments. They have daily water temperature ranges that may be larger than in any other aquatic ecosystem. There are periods in the summer when water temperatures rise above 30 °C and fall close to freezing within a few days. The lack of thermal stratification and potential refugia represents additional stressors for the biological community. Alpine ponds were also frozen solid for most of the year. Finally, alpine ponds have quite variable physical and chemical conditions during the ice-free season, due in part to erratic water volumes and dramatic events such as summer snowstorms and windstorms. These features not only make alpine ponds physically demanding environments but also a unique type of aquatic ecosystem.

Similar to arctic ponds studied in Nunavut (Douglas and Smol 1999), alpine ponds in Banff National Park will likely become even more physically demanding as the climate warms. For instance in a warm-dry year, alpine ponds I studied had warmer mean temperatures, larger daily temperature ranges, more extremely warm temperature events, a longer ice-free season, earlier drying and higher base cations, alkalinity, pH and conductivity than in a cold-wet year. Many of these changes are similar to trends found in European alpine lakes (Psenner and Schmidt 1992; Sommaruga-Wögraph et al. 1997; Koinig et al. 1998) and low elevation boreal lakes (Schindler et al. 1996) during warming periods. However it is still unclear if alpine systems are more affected by climate warming than low elevation systems or how the physical and chemical changes will affect the biological communities in alpine ponds.

Similar to Vinebrooke and Leavitt's (1999) conclusions for alpine lakes, my results suggest that algal communities in alpine ponds may be particularly sensitive to climate change. Chemical variables (DOC, pH and conductivity) that best predict patterns in phytoplankton and epipelon abundance and community composition in alpine ponds, have been linked to climate warming in alpine ponds (Chapter 2) and/or alpine and low elevation lakes (Psenner and Schmidt 1992; Schindler et al. 1996). However, because

interannual variability in the environmental-algal relationships of alpine ponds is large, in order to make realistic predictions on how algal communities will respond to climate warming may require several years of study.

Using nutrient diffusing substrata, I found that total epilithon, chlorophytes and chromophytes were primarily N-limited, whereas Cyanobacteria were slightly P-limited. Total epilithon, chlorophyte and Cyanobacteria abundances and overall community structure were affected more by nutrient enrichment than by invertebrate grazing. However, chromophyte abundance was affected more by invertebrate grazing than by nutrient enrichment. Invertebrate grazing generally decreased epilithon abundance but increased chlorophyte abundance when combined with NP enrichment in early summer. Total epilithon abundance increased in mid-summer as grazer control weakened and water temperature increased, but neither nutrient nor grazing effects were time-dependent. Based on N:P ratios, N-limitation is likely common across alpine ponds in Banff National Park and P-limitation, although rare, likely occurs only in high elevation ponds with rock catchments. Seasonally, P-limitation likely occurs after ice-out and snowstorms. Given the trends of regionally increasing N deposition (Vitousek et al. 1997), evidence of N-limited epilithic algal growth suggests that the majority of these alpine ponds may be vulnerable to increased anthropogenic N deposition.

Since this was the first comprehensive study of alpine ponds in North America, there is much additional research required to fully understand their basic limnology and how it will respond to changing global stressors. Future research should include:

- Because alpine ponds freeze solid in the winter, resident organisms must either have the ability to migrate to suitable overwintering habitats or have mechanisms to avoid or tolerate freezing. We need to determine if this ability to survive winter freezing pre-adapts alpine pond organisms to survive summer desiccation. This is of particular interest given that summer desiccation will likely increase through the Canadian Rocky Mountains and arctic in response to climate change (Intergovernmental Panel on Climate Change 2001).

- In terrestrial communities, brief extreme events are often more important in controlling species distributions than gradual changes in the mean (Easterling et al. 2000; Parmesan et al. 2000). A similar trend has yet to be found in aquatic communities but is quite possible in shallow ponds and streams. We need to determine the effects of extremely cold (<1°C) and warm (>30°C) temperature events on the biological communities in alpine ponds, especially because extreme events are expected to increase in the future in response to climate change (Meehl et al. 2000).
- Alpine ponds had large daily temperature ranges that increased in the warm-dry year. We need to determine the effects of these large DTR on the chemical conditions and biological communities in alpine ponds, especially since they should increase in the future in response to climate change.
- Dissolved organic carbon concentrations in alpine ponds were higher than in alpine lakes but DOC in ponds likely has lower aromaticity due to higher photodegradation in the shallower ponds. However, this has not yet been confirmed. We therefore need to determine DOC quality and depth of UVR penetration in alpine ponds. This is especially important since climate change can decrease DOC concentrations and alter DOC quality, which in turn increase penetration of biologically harmful UVR radiation (Schindler et al. 1996). Given the shallow depths of alpine ponds and the fact they will become even shallower with climate change suggests that any increased in UVR may have significant biological effects.
- I found that alpine ponds were N-limited, whereas a nearby alpine lake is P-limited. We need to determine why N-fixing bacteria do not proliferate in alpine ponds and compensate for N deficiencies, leaving P as the limiting nutrient such as in low elevation lakes (Schindler 1977). One possible reason why N-fixing Cyanobacteria do not proliferate in alpine ponds is that Cyanobacteria are sensitive to turbulence and variable water temperatures, which occur often in alpine ponds. Furthermore, N-fixation may be inhibited in alpine ponds by oxygen saturation (Howarth et al. 1988) and high ultraviolet radiation (Higley et al. 2001).
- Similar to results from other algal-grazer experiments (Cuker 1983; Lowe and Hunter 1988; Power et al. 1988; Marks and Lowe 1989; Rosemond et al. 1993), diatom abundance in alpine ponds was consistently reduced with grazing. A meta-analysis of

all the current algal-grazer experiments should be done to determine if this trend appears throughout the literature.

REFERENCES

Cuker, B.E. 1983. Grazing and nutrient interactions in controlling the activity and composition of the epilithic algal community of an arctic lake. Limnology and Oceanography **28:** 133-141

Douglas, M.S.V. and Smol, J.P. 1999. Freshwater diatoms as indicators of environmental changes in the high Arctic. *In* The Diatoms: Applications for the Environmental and Earth Sciences. *Edited by* E.F. Stoermer and J.P. Smol. Cambridge University Press, Cambridge. pp. 227-44.

Easterling, D.R., Evans, J., Groisman, P.Y., Karl, T.R., Kunkel, K.E. and Ambenje, P. 2000. Observed variability and trends in extreme climate events: A brief review. Bulletin of the American Meterorological Society **81**: 417-425.

Higley, B., Carrick H.I., Brett, M.T., Luecke, C. and Goldman, C.R. 2001. The effects of ultraviolet radiation and nutrient additions on periphyton abundance and composition in a sub-alpine lake (Castle Lake, USA). International Review of Hydrobiology **86:** 147-163.

Howarth, R.W., Marino, R. and Cole, J.J. 1988. Nitrogen fixation in freshwater, estuarine and marine ecosystems: 2. Biogeochemical controls. Limnology and Oceanography **33:** 688-701

Intergovernmental Panel of Climate Change. 2001. Climate Change 2001: The Scientific Basis. http://www.grida.no/climate/ipcc_tar/wg1/index.htm

Koinig, K.A., Schmidt, R., Sommaruga-Wögraph, S., Tessadri, R. and Psenner, R. 1998. Climate change as the primary cause for pH shifts in a high alpine lake. Water, Air and Soil Pollution **104**: 167-180.

Lowe, R.L. and Hunter, R.D. 1988. Effect of grazing by *Physa integra* on periphyton community structure. Journal of North American Benthological Society **7:** 29-36.

Marks, J.C. and Lowe, R.L. 1989. The independent and interactive effects of snail grazing and nutrient enrichment on structuring periphyton communities. Hydrobiologia **185:** 9-17.

Meehl, G.A., Zwiers, F., Evans, J., Knutson, T., Mearns, L. and Whetton, P. 2000. Trends in extreme weather and climate events: Issues related to modeling extremes in projections of future climate change. Bulletin of the American Meteorological Society **81**: 427-436.

Parmesan, C., Root, T.L. and Willig, M.R. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society **81**: 443-450.

Power, M.E., Stewart, A.J. and Matthews, W.J. 1988 Grazer control of algae in an Ozark Mountain stream: Effects of short-term exclusion. Ecology **69:** 1894-1898.

Psenner, R. and Schmidt, R. 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. Nature **356**: 781-783.

Rosemond, A.D., Mulholland, P.J. and Elwood, W. 1993. Top-down and bottom-up control of stream periphyton: Effects on nutrients and herbivores. Ecology **74:** 1264-1280.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science **195:** 260-262.

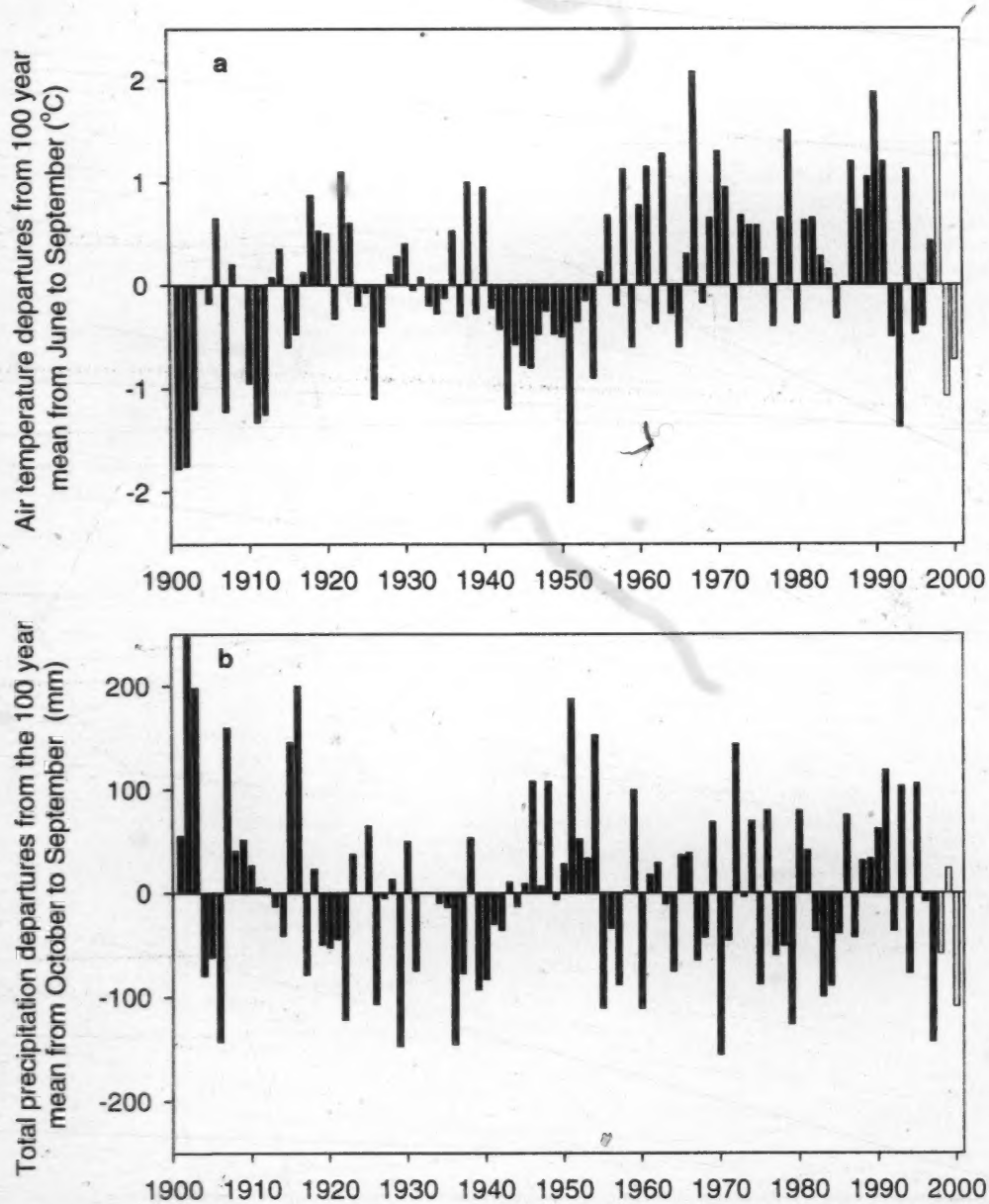
Schindler, D.W., Bayley, S.E. and Parker, B.R. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, Northwestern Ontario. Limnology and Oceanography **41**: 1004-1017.

Sommaruga-Wögraph, S., Koinig, K.A., Schmidt, R., Sommaruga, R., Tessadri, R. and Psenner, R. 1997. Temperature effects on the acidity of remote alpine lakes. Nature **387**: 64-67.

Vinebrooke, R.D. and Leavitt, P.R. 1999. Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. Journal of North American Benthological Society **18**: 14-32.

Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. and Tilman, D.G. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications **7:** 737-750.

APPENDICES



Appendix 1: Mean departures of June to September air temperatures from 100 year mean (a) and total precipitation departures from the 100 year mean for the year leading up to and including the summer (October to September) (b) for Banff town site (Environment Canada 2002). The gray bars are the study years 1998, 1999 and 2000.

Appendix 2: Mean (standard deviation), minimum and maximum values for chemical features measured in the five alpine ponds in 1998 and 1999. Significant differences between 1998 and 1999 for each pond are indicated (* = $P < 0.1$, ** = $P < 0.05$, *** = $P < 0.001$).

	All Ponds	South Ridge Two		East Ridge One	
	1998 and 1999	1998	1999	1998	1999
Ammonium (µg/L)	20.9 (22.9)	21.3 (19.9)	51.5 (46.8)	16.3 (21.0)	14.1 (12.3)
	n.d.-132.7	n.d.-44.0	16.4-132.7	n.d.-52.3	3.1-32.3
Nitrite+Nitrate (µg/L)	8.6 (11.9)	3.8 (2.5)	8.5 (5.5)	2.9 (2.7)	5.8 (3.8)
	0.6-60.6	1.9-7.5	3-17.4	1.1-7.7	1.3-11.3
Dissolved inorganic	29.5 (28.5)	25.0 (21.3)	60.0 (52.0)	19.2 (20.7)	19.9 (13.9)
nitrogen (µg/L)	1.9-150	1.9-47.2	19.4-150	2.0-53.4	5.2-37.4
Total Phosphorus	37.0 (29.1	39.7 (14.3)	43.8 (34.4)	35.3 (24.9)	28.6 (11.3)
(µg/L)	15.5-207.3	23.7-51.4	17.2-99.3	16.6-71.9	16.2-49.4
Total dissolved P	21.2 (23.4)	20.6 (6.0)	25.6 (25.8)	15.2 (7.5)	17.6 (6.7)
(µg/L)	7.1-182.2	13.6-26.1	10.2-71.3	8.0-28.0	10.7-28.2
Soluble reactive P	6.3 (1.3)	4.6 (3.5)	6.8 (8.1)	3.3 (1.4)	6.6 (4.2)
(µg/L)	3.8-9.2	2.5-8.6	1.5-21.2	2.2-5.3	1.6 -13.2
DIN:TP	0.93 (0.99)	0.77 (0.21)	1.38 (0.34)	0.59 (0.23)	0.72 (0.46)
	0.13-7.35	0.53-0.92	1.05-1.90	0.27-0.79	0.21-1.38
Dissolved organic	6.6 (1.3)	6.2 (1.2)	7.5 (0.1)	6.4 (0.14)	6.7 (1.8)
carbon (mg/L)	3.8-9.2	5.3-7.0	7.4-7.5	6.3-6.5	4.8-9.2
Silica (mg/L)	0.81 (0.70)	1.94 (0.20)	1.50 (0.94)	1.56 (0.49)	1.32 (0.59)
	0.05-2.59	1.8-2.09	0.39-2.59	1.01-1.97	0.24-1.88
Chloride (meq/L)	0.038 (0.095)	0.008 (0.003)	0.011 (0.004)	0.173 (0.234)	0.010 (0.002)
	0.004-0.338	0.006-0.010	0.008-0.016	0.007-0.338	0.008-0.013
Sulfate (meq/L)	0.007 (0.004)	0.011 (0.006)	0.200 (0.010)	*0.007 (0.001)	0.026 (0.012)
	0.002-0.015	0.007-0.015	0.013-0.031	0.006-0.007	0.015-0.043
Sodium (meq/L)	0.030 (0.015)	0.028 (0.015)	0.028 (0.014)	0.028 (0.014)	0.031 (0.010)
	0.017-0.060	0.017-0.039	0.020-0.044	0.018-0.038	0.022-0.045
Potassium (meq/L)	0.012 (0.005)	0.014 (0.001)	0.017 (0.011)	0.005 (0.002)	0.006 (0.005)
	0.004-0.020	0.013-0.014	0.005-0.028	0.004-0.006	0.002-0.012
Calcium (meq/L)	0.266 (0.091)	0.31 (0.03)	0.24 (0.15)	0.38 (0.18)	0.32 (0.27)
	0.158-0.509	0.29-0.33	0.14-0.42	0.26-0.51	0.13-0.71
Magnesium (meq/L)	0.293 (0.211)	0.34 (0.04)	0.23(0.17)	0.58 (0.50)	0.26 (0.22)
	0.129-0.930	0.31-0.37	0.12-0.43	0.22-0.93	0.11-0.57
Bicarbonate (meq/L)	0.54 (0.38)	0.60 (0.11)	0.44 (0.25)	0.69 (0.36)	0.60 (0.39)
	0.12-1.58	0.52-0.68	0.22-0.77	0.44-0.95	0.16-1.01
Alkalinity (meq/L)	0.55 (0.40)	0.60 (0.11)	0.44 (0.25)	0.69 (0.36)	0.65 (0.47)
	0.12-1.58	0.52-0.68	0.22-0.77	0.44-0.95	0.16-1.27
pH	7.2 (0.6)	*7.4 (0.3)	6.9 (0.3)	7.8 (0.7)	7.4 (1.0)
	6.2-8.7	7.2-7.6	6.5-7.3	7.1-8.5	6.4-8.7
Conductivity (µS/cm)	61.9 (41.1)	61.9 (10.9)	52.7 (18.4)	84.73 (26.3)	74.5 (43.8)
	12.3-159.9	54.2-69.6	26.3-71.3	45.5-101.0	16.9-156.3

Appendix 2: Continued

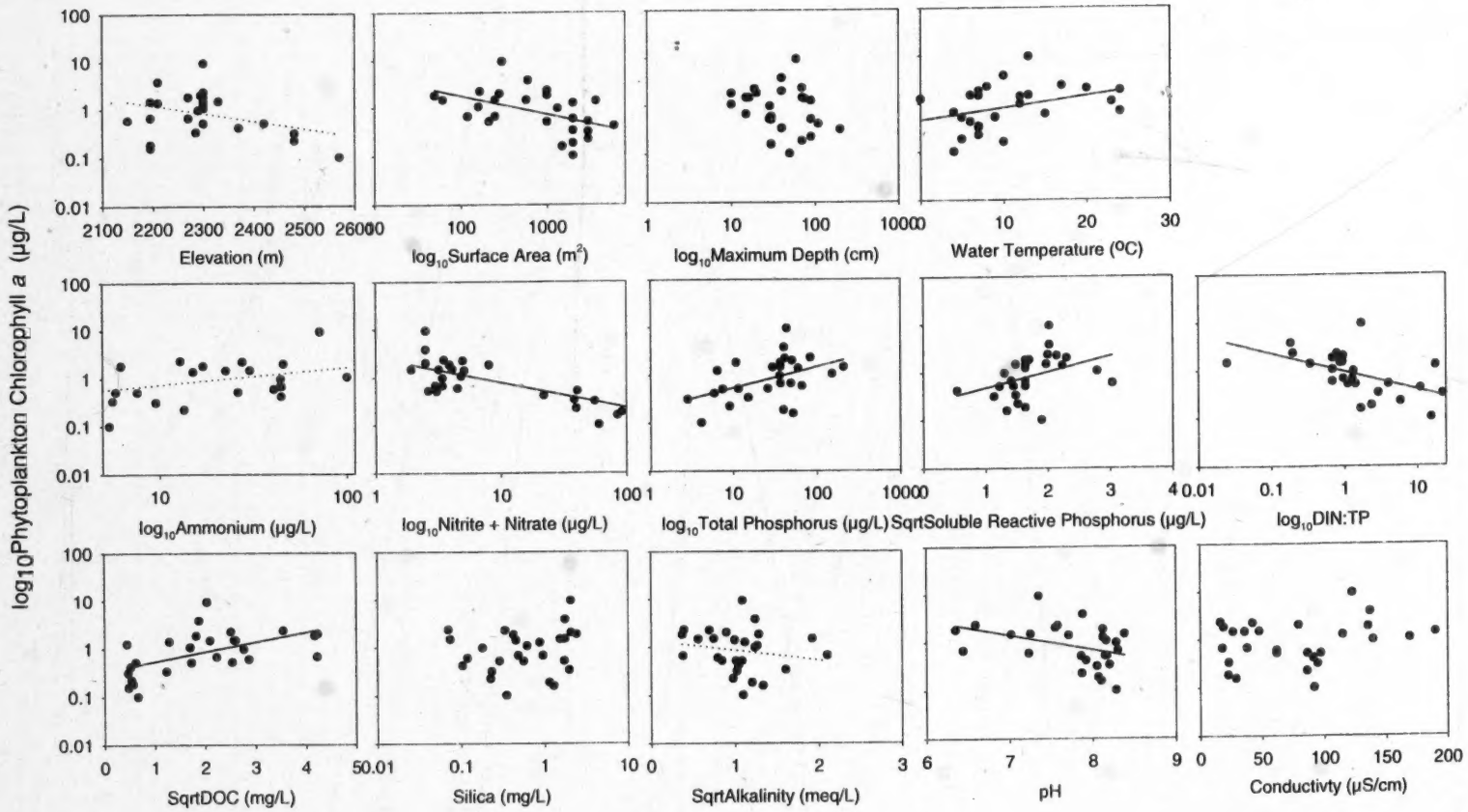
	East Ridge Two		East Ridge Three		Snowflake Pond
	1998	1999	1998	1999	1999
NH_4	23.8 (17.2)	18.7 (14.4)	19.5 (22.4)	19.5 (25.5)	13.3 (11.2)
	9.7-50.9	5.7-45.7	1.3-67.9	1.9-77.5	n.d.-34.0
NO_2+NO_3	11.2 (17.2)	9.7 (6.9)	4.5 (4.8)	20.3 (24.5)	7.0 (5.5)
	2.5-46.2	3.5-22.3	0.6-16.2	2.1-60.6	1.9-16.1
DIN	35.1 (31.9)	28.4 (12.0)	24.0 (23.6)	39.9 (43.1)	20.2 (9.2)
	14.9-97.1	14.4-49.2	1.9-75.4	5.6-133.8	9.8-38.4
TP	*48.1 (19.8)	29.4 (15.3)	55.4 (63.2)	27.3 (11.6)	31.1 (8.1)
	24.7-70.0	17.2-60.8	17.7-207.3	15.5-47.5	18.9-39.6
TDP	50.7 (65.0)	18.9 (7.4)	16.7 (6.0)	14.0 (4.9)	17.6 (4.8)
	13.2-182.2	9.9-32.8	7.8-27.4	7.1-22.4	13.9-28.0
SRP	25.4 (43.1)	5.5 (3.1)	2.9 (1.4)	4.4 (2.8)	2.0 (2.2)
	2.6-102.2	1.3-11.4	1.7-5.3	1.0-8.1	0.6-7.5
DIN:TP	0.50 (0.17)	1.03 (0.35)	0.62 (0.38)	1.81 (2.34)	0.66 (0.24)
	0.25-0.67	0.75-1.53	0.13-1.27	0.14-7.35	0.38-1.07
DOC	6.9 (0.4)	6.9 (1.7)	6.0 (1.4)	5.5 (1.2)	7.7 (0.7)
	6.6-7.2	4.6-9.1	4.6-8.3	3.8-6.9	6.6-8.5
Si	0.81 (0.69)	0.41 (0.28)	0.28 (0.21)	0.37 (0.29)	0.43 (0.29)
	0.14-1.41	0.09-0.82	0.05-0.51	0.14-0.89	0.08-0.83
Cl	0.008 (0.006)	0.011 (0.004)	*0.014 (0.007)	0.007 (0.003)	0.010 (0.004)
	0.004-0.016	0.007-0.016	0.008-0.023	0.003-0.012	0.006-0.015
SO_4	**0.008 (0.004)	0.017 (0.003)	0.005 (0.003)	0.009 (0.006)	0.092 (0.016)
	0.004-0.011	0.014-0.20	0.002-0.010	0.001-0.018	0.073-0.111
Na	0.032 (0.020)	0.032 (0.011)	0.030 (0.017)	0.023 (0.011)	0.023(0.009)
	0.019-0.055	0.021-0.045	0.018-0.060	0.015-0.043	0.012-0.036
K	0.015 (0.006)	0.010 (0.003)	**0.012 (0.004)	0.006 (0.002)	0.062 (0.007)
	0.008-0.020	0.007-0.014	0.009-0.018	0.004-0.008	0.052-0.072
Ca	0.23 (0.02)	0.17 (0.06)	0.22 (0.05)	0.16 (0.05)	1.11 (0.36)
	0.21-0.25	0.11-0.24	0.16-0.28	0.11-0.21	0.63-1.56
Mg	0.22 (0.03)	0.16 (0.06)	*0.20 (0.06)	0.14 (0.04)	0.12 (0.03)
	0.19-0.25	0.09-0.22	0.13-0.27	0.09-0.19	0.09-0.17
HCO_3	**0.43 (0.06)	0.27 (0.10)	**0.40 (0.11)	0.26 (0.10)	1.16 (0.32)
	0.35-0.47	0.13-0.41	0.27-0.51	0.12-0.36	0.60-1.58
ALK	**0.43 (0.06)	0.27 (0.10)	**0.40 (0.11)	0.26 (0.10)	1.17 (0.33)
	0.35-0.47	0.13-0.41	0.27-0.51	0.12-0.36	0.60-1.58
pH	***7.3 (0.3)	6.7 (0.2)	***7.3 (0.2)	6.5 (0.2)	7.8 (0.4)
	7.0-7.7	6.2-6.9	6.9-7.4	6.2-6.8	7.3-8.3
Cond	***44.2 (7.7)	32.8 (8.7)	***42.3 (9.4)	24.9 (5.9)	123.6 (20.7)
	34.0-52.3	15.2-44.5	28.1-51.5	12.3-32.7	75.2-159.9

Appendix 3: Physical, chemical, biological variables measured in 14 ponds sampled in 1999 and 28 ponds sampled in 2000 in Banff National Park, Canada. Blank space indicate that no sample was taken.

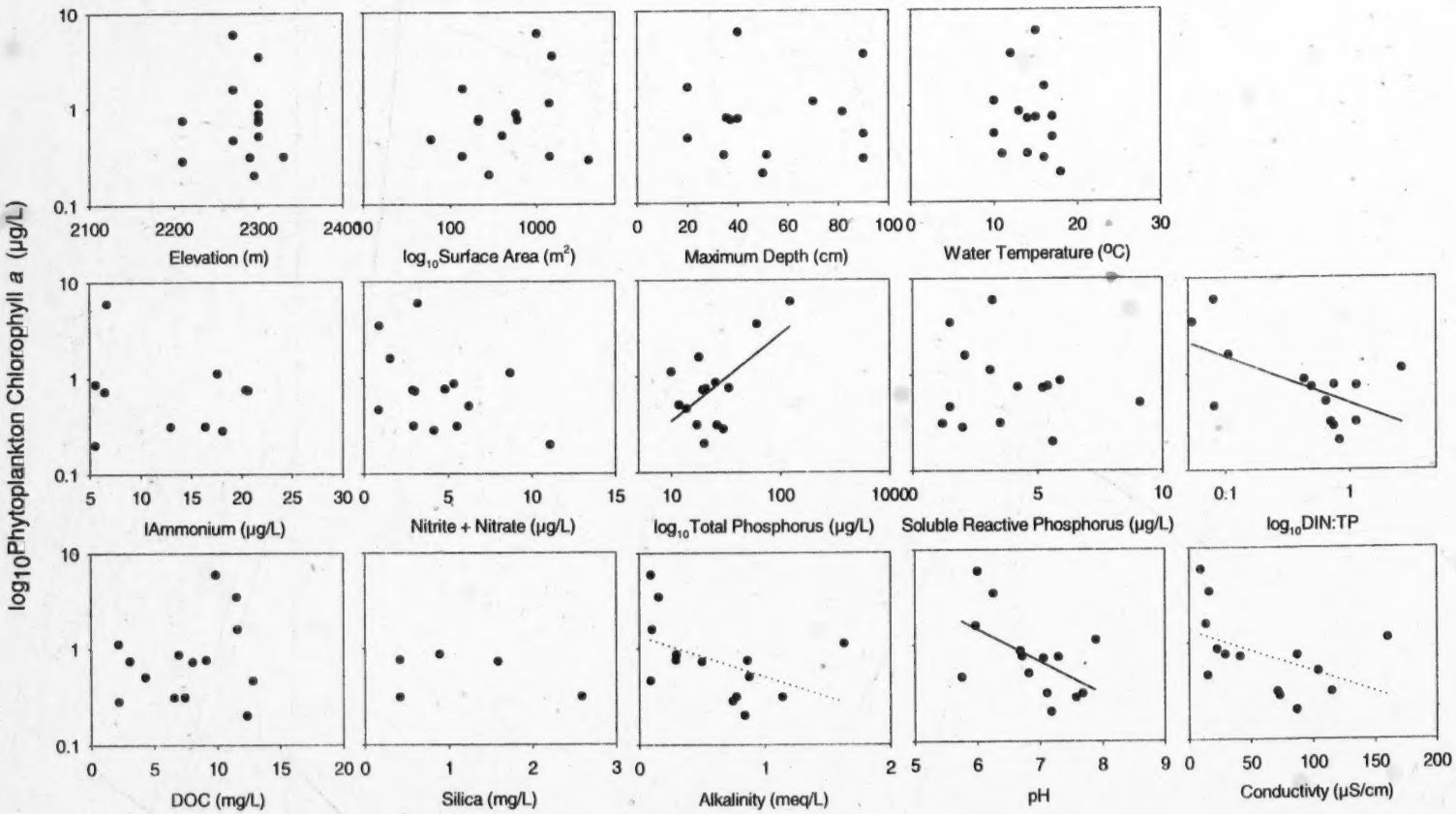
POND	YEAR	ELV	AREA	DEPTH	BOTT	DRBN	WTEMP	DOC	COND	ALK
CL	1999	2210	4000.0	90	Sediment	Meadow	16	2.20	73.0	0.76
CS	1999	2210	600.0	40	Sediment	Meadow	15	3.07	87.0	0.90
ER1	1999	2300	213.0	37	Sediment/rock	Meadow	14	8.05	41.1	0.51
ER2	1999	2300	215.7	36	Sediment/rock	Meadow	17	9.13	29.2	0.30
ER3	1999	2300	574.3	82	Sediment/rock	Meadow	13	6.93	22.5	0.30
ER4	1999	2295	280.0	50	Sediment	Meadow	18	12.34	86.8	0.85
GP	1999	2300	1500.0	90	Sediment	Meadow	12	11.53	16.2	0.16
NP1	1999	2270	1000.0	40	Sediment	Meadow	15	9.90	9.3	0.10
NP2	1999	2270	140.0	20	Sediment	Meadow	16	11.60	13.4	0.10
NP3	1999	2270	60.0	20	Sediment	Meadow	17	12.80	15.1	0.09
SFP	1999	2290	1416.2	51	Sediment/rock	Meadow	11	6.57	115.0	1.16
SG3	1999	2300	400.0	90	Sediment	Meadow	10	4.30	103.9	0.89
SPC	1999	2300	1400.0	70	Sediment/rock	Meadow	10	2.19	160.0	1.66
SR2	1999	2330	138.0	35	Sediment/rock	Meadow	14	7.41	71.3	0.79
BE	2000	2195	2000.0	70	Sediment	Meadow/rock	5	0.32	22.5	1.48
BML	2000	2195	250.0	15	Sediment	Meadow/rock	13	6.78	35.8	3.64
BMS	2000	2195	250.0	15	Sediment	Meadow/rock	4	4.98	37.6	4.46
BW	2000	2195	1500.0	30	Sediment	Meadow	10	0.23	28.9	1.82
CL	2000	2210	3700.0	75	Sediment	Meadow	12	1.65	190.0	1.01
CS	2000	2210	600.0	40	Sediment	Meadow	10	3.51	136.8	1.57
DP	2000	2570	2000.0	50	Sediment/rock	Meadow/rock	4	0.44	91.9	1.23
ER1	2000	2300	213.0	29	Sediment/rock	Meadow	9	6.45	61.7	0.73
ER2	2000	2300	166.7	19	Sediment/rock	Meadow	8	6.32	42.1	0.49
ER3	2000	2300	574.3	71	Sediment/rock	Meadow	7	4.41	26.2	0.32
ER4	2000	2295	280.0	40	Sediment	Meadow	20	17.93	79.3	0.82
GP	2000	2300	1000.0	70	Sediment	Meadow	17	12.61	16.2	0.16
HNE	2000	2480	3000.0	90	Sediment/rock	Meadow/rock	7	0.29	86.1	0.97
HNW	2000	2480	3000.0	200	Sediment/rock	Rock	7	0.22	94.7	1.07
HS	2000	2420	3000.0	90	Rock	Rock	5	0.38	86.4	1.05
MDL	2000	2300	2000.0	90	Sediment/rock	Meadow/rock	0	0.20	114.8	1.27
MDS1	2000	2300	1000.0	30	Sediment	Meadow	9	2.98	97.2	1.19
MDS2	2000	2300	1000.0	20	Sediment	Meadow	7	3.33	135.3	1.68
NP1	2000	2270	1000.0	35	Sediment	Meadow	18	10.78	11.1	0.14
NP2	2000	2270	120.0	15	Sediment	Meadow	24	17.81	17.7	0.15
NP3	2000	2270	50.0	10	Sediment	Meadow	24	17.39	18.8	0.14
PIP	2000	2370	6000.0	110	Sediment/rock	Rock	6	0.27	91.3	1.11
PP2	2000	2285	2000.0	40	Sediment	Meadow	7	1.51	23.1	2.63
SFP	2000	2290	1322.7	29	Sediment/rock	Meadow	12	7.67	139.4	1.56
SG3	2000	2300	300.0	60	Sediment	Meadow	13	4.15	122.6	1.21
SPC	2000	2300	160.0	10	Sediment/rock	Meadow	23	2.90	169.1	1.63
SR2	2000	2330	61.9	16	Sediment/rock	Meadow	6	6.65	47.6	0.57
TP	2000	2150	2000.0	30	Sediment	Meadow	15	8.22	61.6	0.65

Appendix 3: Continued

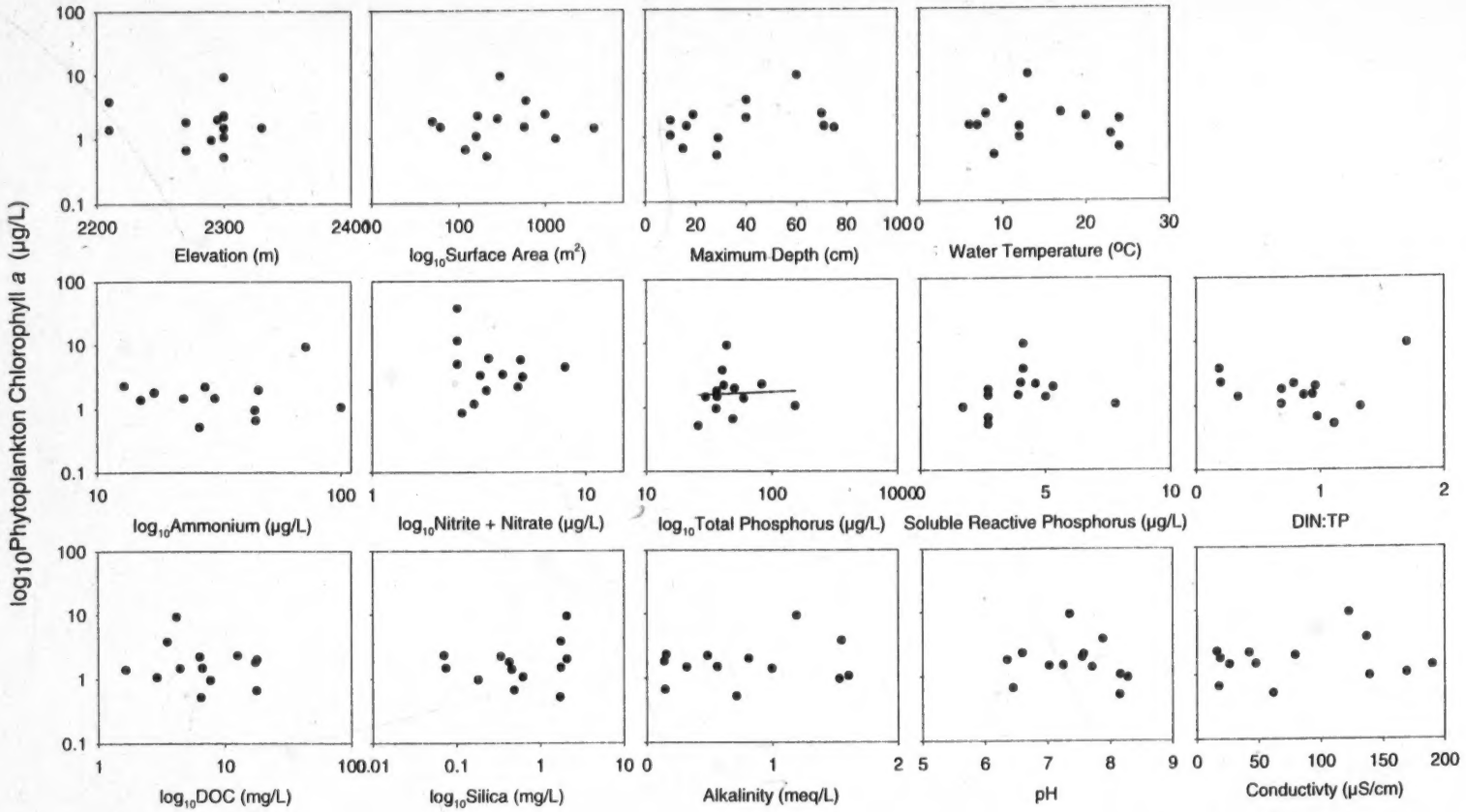
POND	YEAR	pH	NH3-N	NO2-N+ NO3-N	DIN	TP	SRP	DIN:TP	Si	Chl *a*P	Chl *a*E
CL	1999	7.58	18.11	4.17	22.28	30.0	2.0	0.74		0.28	0.44
CS	1999	7.29	20.63	2.92	23.55	20.8	4.2	1.13		0.74	4.86
ER1	1999	7.05	6.48	3.04	9.52	19.4	5.2	0.49	1.59	0.72	2.93
ER2	1999	6.71	20.37	4.82	25.19	33.7	5.4	0.75	0.42	0.76	3.25
ER3	1999	6.68	5.56	5.36	10.92	25.4	5.9	0.43	0.89	0.86	1.53
ER4	1999	7.18	5.52	11.10	16.62	20.1	5.6	0.83		0.20	0.07
GP	1999	6.25	2.33	0.92	3.25	60.7	1.5	0.05		3.46	1.01
NP1	1999	6.00	6.71	3.21	9.92	123.2	3.2	0.08		5.94	1.47
NP2	1999	5.97	0.32	1.57	1.89	17.9	2.1	0.11		1.59	0.27
NP3	1999	5.75	0.24	0.88	1.12	13.8	1.5	0.08		0.46	1.35
SFP	1999	7.68	12.96	5.54	18.50	26.3	1.2	0.70	0.42	0.31	1.38
SG3	1999	6.82	1.35	6.25	7.60	11.8	9.1	0.64		0.51	1.01
SPC	1999	7.89	17.60	8.72	26.32	10.0	3.1	2.63		1.11	0.61
SR2	1999	7.11	16.41	2.95	19.36	17.2	3.5	1.13	2.59	0.31	0.13
BE	2000	8.07	0.66	92.88	93.54	39.9	2.7	2.34	1.15	0.18	21.17
BML	2000	8.38	3.23	1.92	5.15	209.0	2.2	0.02	1.54	1.47	3.91
BMS	2000	8.30	44.03	3.41	47.44	36.9	2.0	1.29	0.96	0.67	15.43
BW	2000	8.10	2.17	84.96	87.13	51.9	1.8	1.68	1.29	0.16	25.64
CL	2000	7.71	15.10	5.06	20.16	59.7	5.0	0.34	0.45	1.39	0.67
CS	2000	7.88	4.95	2.50	7.45	40.4	4.1	0.18	1.76	3.80	6.98
DP	2000	8.28	5.42	60.60	66.02	4.2	3.6	15.72	0.35	0.10	
ER1	2000	8.15	26.29	2.63	28.92	26.0	2.7	1.11	1.73	0.52	7.23
ER2	2000	7.58	27.67	4.94	32.61	41.5	4.6	0.79	0.34	2.23	9.38
ER3	2000	7.02	22.61	3.20	25.81	29.8	2.7	0.87	0.07	1.47	2.93
ER4	2000	7.55	45.84	2.50	48.34	50.4	5.3	0.96	2.08	2.00	6.98
GP	2000	6.59	12.91	3.50	16.41	83.2	4.0	0.20	0.07	2.32	4.14
HNE	2000	7.87	13.56	39.97	53.53	9.1	2.3	5.88	0.23	0.22	
HNW	2000	8.05	9.56	56.13	65.69	2.9	1.3	22.65	0.23	0.32	12.21
HS	2000	8.17	5.86	40.67	46.53	11.6	2.1	4.01	0.29	0.52	
MDL	2000	8.12	4.96	111.91	116.87	6.5	2.7	17.98	0.88	1.26	39.31
MDS1	2000	7.86	7.63	3.06	10.69	7.5	1.5	1.43	0.56	0.51	2.52
MDS2	2000	8.12	6.25	3.88	10.13	10.9	2.9	0.93	2.42	1.83	11.60
NP1	2000	6.46	18.36	4.00	22.36	272.3	6.6	0.08	0.05	27.86	3.91
NP2	2000	6.44	44.69	3.00	47.69	48.9	2.7	0.98	0.49	0.66	30.01
NP3	2000	6.35	17.14	8.00	25.14	36.5	2.7	0.69	0.43	1.82	6.30
PIP	2000	7.92	44.62	22.00	66.62	6.0	0.3	11.10	0.10	0.42	7.26
PP2	2000	8.20	5.65	38.62	44.27	15.2	2.2	2.91	1.98	0.34	1.59
SFP	2000	8.28	44.29	3.42	47.71	36.0	1.7	1.33	0.18	0.97	5.45
SG3	2000	7.35	71.69	2.50	74.19	43.7	4.1	1.70	2.08	9.35	3.07
SPC	2000	8.16	100.16	4.80	104.96	152.8	7.8	0.69	0.62	1.07	2.00
SR2	2000	7.25	30.37	4.08	34.45	36.7	3.9	0.94	1.76	1.49	4.24
TP	2000	7.23	40.86	4.50	45.36	66.5	9.2	0.68	0.12	0.59	10.67



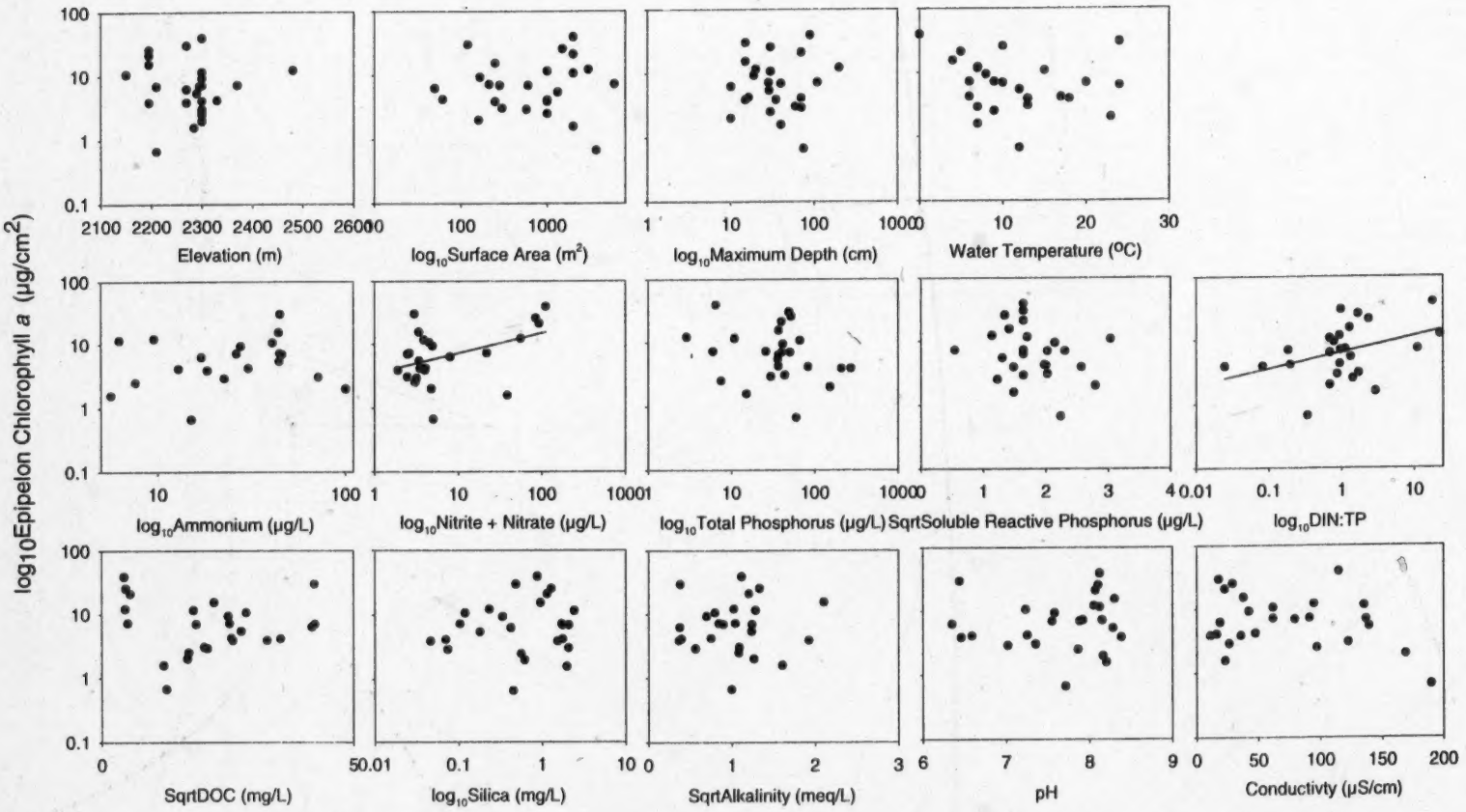
Appendix 4: Phytoplankton abundance (chlorophyll *a*) – environmental relationships in the 28 ponds sampled in 2000. Significant relationships ($P < 0.05$) are indicated with solid lines and weak relationships ($0.05 < P < 0.1$) are indicated with a dotted line.



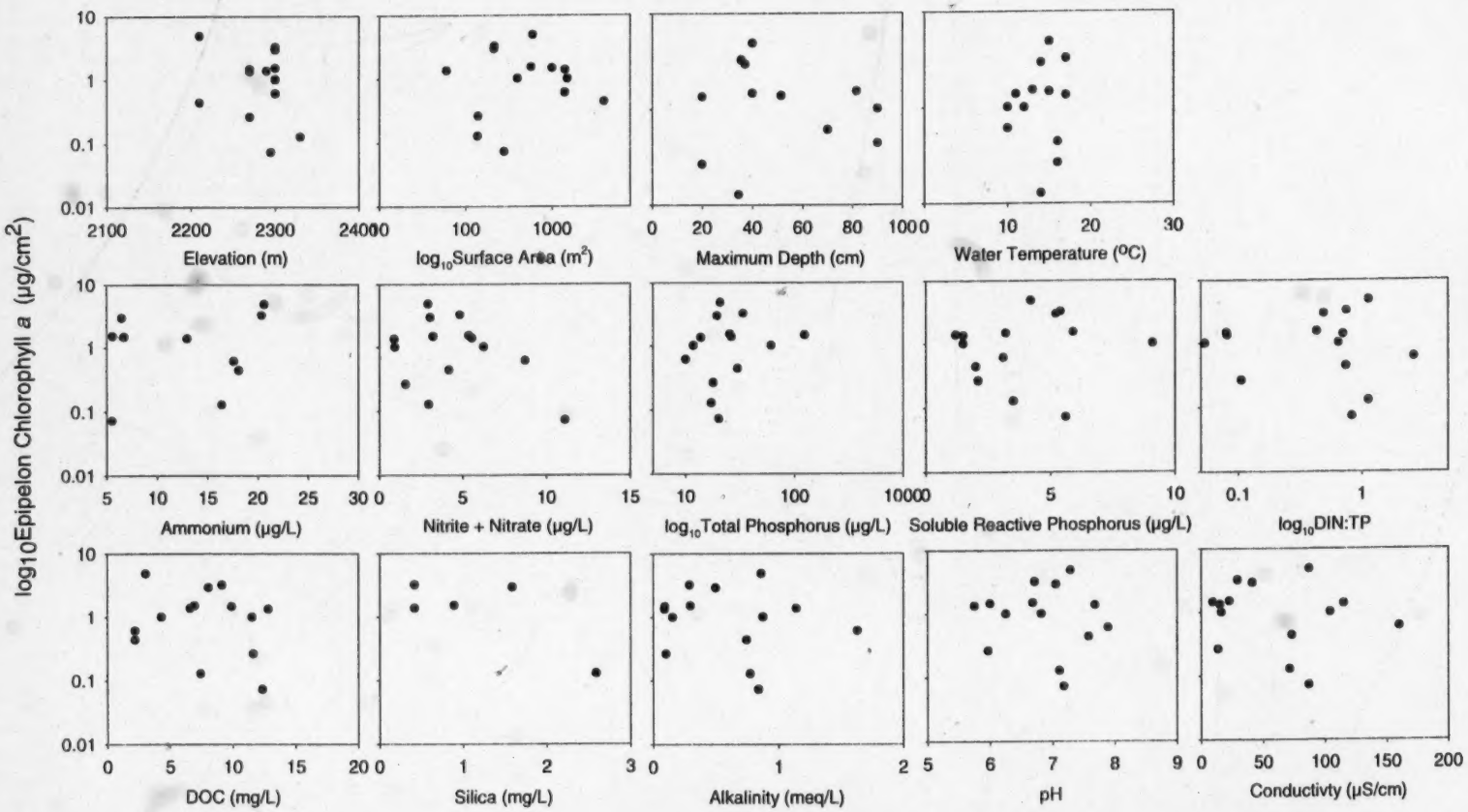
Appendix 5: Phytoplankton abundance (chlorophyll *a*) – environmental relationships in the 14 ponds sampled in 1999. Significant relationships ($P < 0.05$) are indicated with solid lines and weak relationships ($0.05 < P < 0.1$) are indicated with a dotted line.



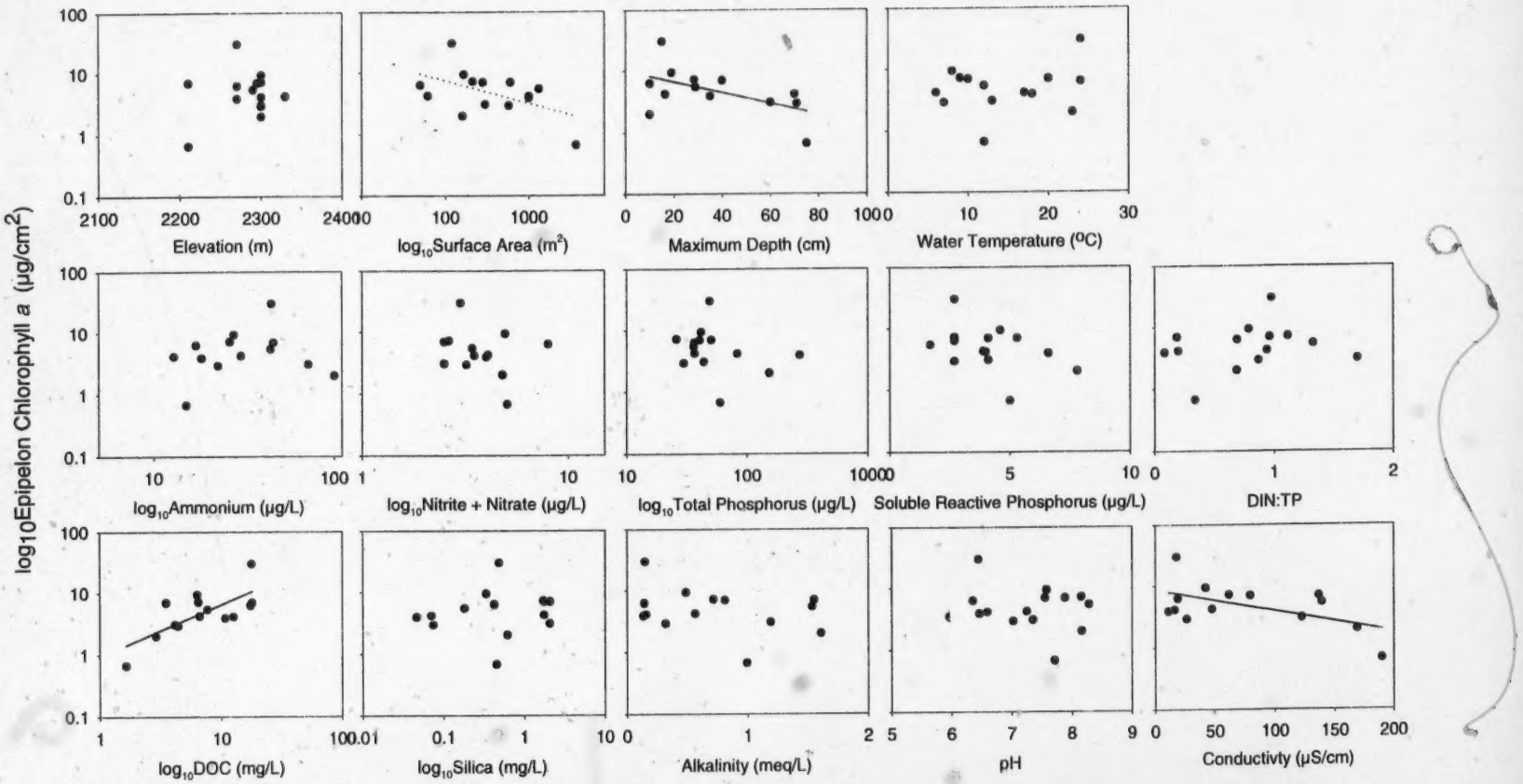
Appendix 6: Phytoplankton abundance (chlorophyll *a*) – environmental relationships in the 14 ponds sampled in 2000. Significant relationships ($P < 0.05$) are indicated with solid lines and weak relationships ($0.05 < P < 0.1$) are indicated with a dotted line.



Appendix 7: Epipelon abundance (chlorophyll *a*) – environmental relationships in the 28 ponds sampled in 2000. Significant relationships ($P < 0.05$) are indicated with solid lines and weak relationships ($0.05 < P < 0.1$) are indicated with a dotted line.



Appendix 8: Epipelon abundance (chlorophyll *a*) – environmental relationships in the 14 ponds sampled in 1999. Significant relationships ($P < 0.05$) are indicated with solid lines and weak relationships ($0.05 < P < 0.1$) are indicated with a dotted line.



Appendix 9: Epipelon abundance (chlorophyll *a*) – environmental relationships in the 14 ponds sampled in 2000. Significant relationships ($P < 0.05$) are indicated with solid lines and weak relationships ($0.05 < P < 0.1$) are indicated with a dotted line.